EFFECTS OF WATER STRESS ON PINEAPPLE

[*ANANAS COMOSUS* (L.) Merr.)]

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INTRODUCTION

The effects of water stress on physiological processes of plants has been one of the most rapidly expanding areas of research in plant-water relations. The increasing demand for knowledge in this field has been stimulated, at least in part, from increasing realization that in situations where the fertility of soil was not a limiting factor, plant growth, yield, and quality were reduced more often than not by deviations from an optimum plant-water balance. Much of the progress in the field of plant-water relations in the past consists of developing a better understanding of existing concepts, improvements in instrumental techniques for measuring plant and soil water status, and increased emphasis on quantitative study of the various physiological phenomena (Kramer, 1974).

Plant species differ significantly in their ability to withstand the effects of water stress. The classification of plants on the basis of their water relationships as hydrophytes, mesophytes, and xerophytes, provides a means of grouping plant species according to their adaptation and distribution in various moisture regimes. Although the literature on the effects of water stress on plants is voluminous, a clear and quantitative understanding of its effects on specific crop species at various stages of development generally has not been established. This understanding is of particular importance to agricultural

production as it serves as a useful guide for irrigation and other cultural practices.

Pineapple, Ananas comosus (L.) Merr., has unique anatomical and physiological modifications which enable the plant to survive periods of water stress (Ekern, 1965; Krauss, 1948; Neales et al., 1968; Seshagiri and Suryanarayanamurthy, 1957). Under drought conditions, the plants are as hardy as cactus (Sideris and Krauss, 1928). For these and other reasons, the pineapple is one of the few crop plants that can be classified as a true xerophyte (Bartholomew and Kadzimin, 1975). In areas where water is limiting, the effects of water stress on the growth and yield of pineapple are of particular interest. To date, there are no published data which would allow the prediction of growth and yield reductions of this crop as a result of varying levels of water stress.

The objective of this study was to examine the effects of water stress in this crop plant focusing mainly on responses in vegetative tissue. We attempted to follow the trend in leaf water potential, relative water content, and leaf resistance on plants exposed to five levels of soil moisture. Leaf resistance data were also collected for well-watered plants growing in the field for comparative purposes.

REVIEW OF LITERATURE

The growth and development of a plant depends on a number of interconnecting factors. Basically, it depends on continued cell division and on progressive tissue differentiation and expansion until the characteristic form of the plant is recognized. Related to this phenomenon of growth and development are processes which involve the uptake of nutrients from the plant's growth medium, the synthesis of metabolites, and the transport of substances within the plant body.

These physiological processes of the plant take place effectively in an aqueous medium, and since water is the primary transport agent or reactant in many of these processes, reduction in water uptake and dehydration can have deleterious effects. When a plant enters a state where the water status is unfavorable for optimum growth, it may be said to be under water stress (Taylor, 1968). Thus, the internal water balance forms an essential feature in plant-water relations as it controls those physiological processes and conditions which in turn determine the quantity and quality of growth, development, and yield.

Plant-water balance, in turn, is affected by a complex combination of plant, soil, and atmospheric factors. Most crop plants are subjected to some degree of water stress sometime during their life span. Even plants growing in soil at field capacity or in solution cultures can be under water stress on

sunny days (Kramer, 1963). This situation exists because plant water stress develops as a result of excessive rate of water loss, inadequate rate of absorption of water, or a complex combination of the two.

The effects of water stress on plant growth and development can only be determined by direct measurement of the stressed plant. There have been a number of plant characteristics used to indicate plant water status, including water potential, relative water content, and leaf diffusion resistance. Each of these indicators will be discussed under separate sections.

WATER POTENTIAL

The water potential of a plant cell, tissue of organ may be defined by the following equation (Kramer, 1974):

$$\psi = \psi_s + \psi_m + \psi_p \quad (1)$$

where ψ is the total water potential of the system, ψ_s is the solute or osmotic component, ψ_m is the matric compoment, and ψ_p is the turgor or pressure component. These three components of the total water potential represent the principal forces affecting the energy status of water in plant tissues. Water potential is probably the most accurately measured indicator of plant water stress, and has been shown to be correlated with plant processes. A decrease in one of the components is often accompanied by a concurrent decrease in all of the others.

Because of this relationship, any plant process correlated with water potential will also be correlated with osmotic potential or turgor potential. Each of these components will be discussed in separate sub-sections.

Plant water potential has been widely accepted as a fundamental measure of plant water status (Hsiao, 1973). The importance of measurements of plant water potential lies in the fact that it is based on energy associated with water. This energy concept has been indicated by Boyer (1969) to be a convenient means of characterizing water status as it is relatively unaffected by physiological and morphological variations. Efforts to estimate water potential of plant tissue have taken several approaches. However, an examination of the literature indicates that only a limited number of techniques have been widely used.

Although accuracy in estimating the water potential of a system tends to vary with method of measurement, values reported in the literature parallel one another sufficiently so that any one method can be adapted to a particular experiment. For example, Chapman (1970b), using apple leaf discs, found good agreement between the dye method of Shardakov (1953) and the vapor equilibration technique described by Slatyer (1958). Boyer (1969), Boyer and Ghorashy (1971), and De Roo (1969) reported that measurements with the pressure chamber technique paralleled those with the psychrometer technique over much of the water potential range.

The movement of water across a cell membrane and from

cell to cell follows the direction of decreasing water potential. Since plant tissues generally have low water potentials relative to the soil, movement of water into the plant is also along a water potential gradient. Water movement in soil also occurs along water potential gradients (Slatyer, 1967).

Some measurements of leaf water potential reported in the literature show that the values vary tremendously with species and growing conditions. Under conditions of high radiation and adequate water supply, Reicosky et al. (1975) found that the upper limit of leaf water potential was about -2 bars and the lower limit between -18 and -20 bars. This work showed that total water potential in corn, and presumably in other mesophytes, is constantly changing. The term 'threshold' (Hsiao, 1973) or 'critical' (Turner, 1974) level is often used in discussions of water potential and could be defined as the leaf water potential below which the stomata close and leaf diffusive resistance increases rapidly. Threshold leaf water potential values have been reported to vary with species : -6 bars in onion (Millar et al., 1971), -10 to -12 bars in soybean (Boyer, 1970b), -12 to -16 bars in grapevine (Kriedmann and Smart, 1971), -13 bars in tobacco, -17 bars in maize, -20 bars in sorghum (Turner, 1974). Szarek et al. (1973) reported that stressed Opuntia plants had water potentials of -12 to -16 bars and under these conditions, had essentially no net carbon dioxide uptake. After a rain, stem water potentials quickly rose to -6 to -7 bars and net assimilation

of carbon dioxide was observed. The above data contrasts with that of van den Driessche et al. (1971) who reported that in brigalow, a xerophytic Acacia species, stomata remained partly open at -50 bars. At this level of water potential, the leaves were still transpiring and had a measurable photosynthetic rate.

A widely held notion is that low water potential values represent an adaptation to drought (Kramer, 1969; Noy-Meir and Ginzburg, 1969; Turner, 1974). The previously cited data demonstrate that mechanisms of adaptation to drought vary with species. Succulents, such as cactus which are known to survive extreme aridity, apparently do so by suspending water loss rather than being subjected to low levels of plant water potential. The data of Szarek et al. (1973) show that stressed cactus plants had a higher water potential than brigalow (van den Driessche et al., 1971), which is adapted to arid conditions by being able to withstand very low levels of plant water potential.

There are very few data on the relationship between water stress and leaf water potential for pineapple. Wambiji and El-Swiafy (1974) reported that growth of pineapple plants in soil salinized to various levels resulted in a linear decrease in leaf water potential from high to low values in the range of -20 to -30 bars. Their data suggest that pineapple may be intermediate between cactus and brigalow in conserving water in storage tissues and surviving at relatively low leaf water potentials.

Osmotic Potential

Osmotic potential is that component of total water potential which arises from solute effects. Within the tissues of living plants, osmotic potential is the primary component in cell vacuoles and possibly in the cytoplasm as well (Brown, 1972; Noy-Meir and Ginzburg, 1967). Initial decreases in plant water potential are due primarily to changes in turgor potential. Changes in osmotic potential are small until turgor potential reaches zero after which decreases in plant water potential are due primarily to decreases in osmotic potential (Hsiao, 1973). The small decrease in osmotic potential with decreasing plant water potential caused Barrs (1968) to conclude that osmotic potential was a relatively insensitive index of plant water status.

All biochemical reactions in a plant system are probably influenced by the osmotic potential. Salts and osmotic media are commonly used to withdraw water from protein and enzymes. Changes in enzyme hydration will therefore influence their activity (Flowers and Hansen, 1969). Boyer (1965) observed that the photosynthetic rate of salt-stressed cotton leaves declined with increasing NaCl concentration.

It is well known that the osmotic potential of individual cells in tissues varies widely with species. The osmotic potential of soybean leaves under optimum water conditions has been reported to range between -6 to -13 bars (Boyer, 1968). In contrast to this finding, Waisel (1972) cited osmotic potential values ranging from

-12 to -41 bars for a number of halophytes at stress levels between -4 and -28 bars.

Turgor Potential

The pressure or turgor potential is a component of the total water potential that results from the effects of positive water pressure against the plasma membrane and the cell walls (Brown, 1972).

Cell enlargement or cell elongation is dependent on a positive turgor potential (Kramer, 1969). Reduction in turgor causes a reduction in shoot and root elongation and leaf enlargement. Turgor potential also determines the rigidity of plant parts, and therefore, is an important factor in their display. Herbaceous stems, young roots, leaves, flower parts, fruits and buds all owe their form to a positive turgor potential. At zero turgor, wilting and stomatal closure occur. In the case of a leaf, this is followed by a reduction in exposed photosynthetic surface and hence a reduced heat load in an intense solar radiation environment. Wilting and stomatal closure promote recovery of positive turgor because of a reduction in transpiration rate and in the vapor pressure gradient between leaf and air.

Stomatal opening is directly mediated by turgor pressure of guard cells (Meidner and Mansfield, 1968). A reduction in turgor potential would therefore result in reduction of photosynthesis and transpiration. Kramer (1969) indicated that the rate of apparent

photosynthesis is zero at approximately zero turgor.

Turgor potential values for well-watered leaves may be of the order +5 to +9 bars (Barrs, 1968; Boyer, 1968; Gardner and Ehlig, 1965; Kanemasu and Tanner, 1969). When wilting occurs, the turgor potential may drop to or below zero (Wilson, 1967b; Noy-Meir and Ginzburg, 1967). Slatyer (1957) reported that at permanent wilting, tomato and cotton had turgor potential values of -5 and -10 bars respectively. Turner (1974) also reported turgor potentials of -5 bars in the basal leaves of maize, tobacco and sorghum grown in a medium at low water potential of approximately -7 bars.

Matric Potential

The matric component of plant water potential arises from interactions between water molecules and colloidal surfaces. In plant cells, matric forces arise from forces of capillarity, desorption and hydration (Brown, 1972). In well-watered leaves and fleshy tissues, the matric component is very close to zero and only becomes significant numerically when plants are extremely dessicated (Hsiao, 1973). Reviews of Brown (1972), Hsiao (1973) and Wilson (1967a) show that the importance of matric potential increases as leaf water content decreases because the remaining water is more tightly held by colloids and in capillaries. This generalization has several implications in both ecological and physiological studies.

In attempts at understanding the array of adaptation of

plants to survive in xeric environments, the importance of matric potential may have been overlooked. Boyer (1967b) and Wilson (1967a) showed that matric potential can contribute significantly to total water potential of some plants at reduced water content. The development of low matric potential was related to the ratios of cell wall volume to total water volume in the cell and water volume outside of protoplasts to total leaf water volume.

RELATIVE WATER CONTENT

Relative water content (RWC), originally described by Weatherley (1950) as relative turgidity, is another commonly used indicator of plant water status. Relative water content may be defined by the following equation:

$$RWC = (FW - DW)/(TW - DW) \times 100 \qquad (2)$$

where RWC is the relative water content, FW is the initial fresh weight, TW is turgid weight, and DW is dry weight (Barrs and Weatherley, 1962). Relative water content is therefore an estimate of water content rather than water potential.

It has been suggested that RWC could be a useful indicator of plant water status and its use in the field has been recommended (Barrs, 1968; Catsky, 1959; Chapman, 1973; Slatyer, 1955, 1967; Weatherley, 1951). Chapman (1973) indicated that, provided a RWC-water potential relationship was established, RWC could be used to estimate leaf water potential. Slatyer (1960) reported that RWC of Acacia aneura was about 90 percent at a water potential of -20

bars while RWC of tomato was only 50 percent at the same water potential. Also, RWC of sorghum was 84 percent at a water potential of about -13 bars but that of corn was only 55 percent at the same water potential. Although RWC has been shown to be related to plant water potential, it is unsatisfactory for comparative purposes because it varies with the species, the age of the tissue, and conditions under which the plant was grown. In certain plants, no effect of water stress on RWC was apparent indicating that RWC is a poor criterion for evaluating plant water status (Hsiao, 1973; Slatyer, 1960). One major disadvantage of the RWC technique is that it is time consuming (Smart and Bingham, 1974). The measurement involves at least 3 separate readings, a few hours of equilibration time, surface drying of leaf discs, and an oven drying. On that account, results from a particular sampling would not be available until the next day.

Another major shortcoming is that RWC is a rather insensitive indicator of water status when water stress is severe (Hsiao, 1973). In many studies, variations in RWC were small (Barrs, 1968). This is because a small change in water content could affect the turgor potential and hence cause a relatively large change in total water potential. The same change in water content could only cause a change of several percentage points in RWC. For this reason, in other studies RWC showed no significant change while the physiological processes were affected markedly (Hsiao, 1970).

LEAF DIFFUSION RESISTANCE

Stomata respond to several environmental parameters including solar radiation, internal carbon dioxide concentrations, humidity gradients, temperature, and soil moisture (Hall and Kaufmann, 1975). The interaction between stomata and these parameters are not fully understood. In addition, stomatal control mechanisms have been a subject of controversy. Nevertheless, the effects of water deficit in the soil seem to be better understood (Gardner, 1960). As soil water content decreases, the soil and leaf water potentials also decrease; consequently, water stress develops due to water deficit in the plant. When water deficits develop in the leaves, the guard cells lose turgor and the stomata close, thus increasing the diffusive resistance to water vapor transport through the leaves (Kanemasu and Tanner, 1969; Meidner and Mansfield, 1968).

Leaf diffusion resistance may be defined as the total resistance encountered by water molecules in moving from inside a leaf to the atmosphere. Measurement of changes in diffusive resistance are easily made. Leaf resistance is measured by exposing a small portion of a leaf surface to a lithium chloride or other electrical resistance humidity sensor which is sensitive over a narrow range of relative humidity. The sensor is generally housed in a cup and in operation, the cup is first dried (by introducing dry air) and then placed over the leaf. As transpiration proceeds, the humidity in the cup builds up. The electrical resistance change of the sensor as indicated by changing current flow on a microammeter over a

specified span is timed. The rate of change can be interpreted in terms of diffusion resistance. Various modifications of the original Wallihan (1964) design and calibration procedures have been reported (Kanemasu et al., 1969; Stigter et al., 1973; Stiles, 1970; Turner and Parlange, 1970; Wallihan, 1964; van Bavel et al., 1965). However, quantitative relationships between leaf resistance and plant water potential and RWC are necessary if leaf resistance is to be a suitable indicator of plant water requirements.

Much of the recent leaf diffusion resistance data have given a more quantitative basis to relationships between leaf resistance and leaf water status. Hsiao (1973) indicated that most data have demonstrated a threshold level or critical level of water potential or RWC above which leaf resistance remained constant. Slatyer (1967) suggested that leaf resistance may not be greatly affected until a critical leaf water potential is reached. The data of Ehlig and Gardner (1964) also suggested that at least in the detached leaves, stomatal closure caused by water stress occurred within a narrow range of leaf water potentials.

Leaf resistance must also be related to soil water supply if measurements of diffusive resistance are to be used to indicate the need for irrigation. Brady et al. (1975) reported that leaf resistance measurements eliminate the need for a determination of root depth and extraction patterns needed with soil moisture data to estimate when soil water is limiting. Also, within the range of

soil moisture tested by various workers (Jordan and Ritchie, 1971; Kanemasu and Tanner, 1969; Kriedmann and Smart, 1971; Millar et al., 1971; Troughton, 1969), leaf resistance continued to increase with soil water deficit without signs of levelling off. However, these findings probably cannot be generalized for all plant species as there have been indications that some plant species are more sensitive to small water deficits than others (Boyer, 1970b; El-Sharkawy and Hesketh, 1964; Fischer et al., 1970; Millar et al., 1971; Stalfelt, 1961). Brigalow, a xerophytic Acacia species represents an extreme example. The plant was reported to be able to continue normal metabolism even at a water potential value too low for mesophytes to be able to remain viable (van den Driessche et al., 1971).

Apart from species differences, the growing environment strongly influenced stomatal response to water stress (Hall and Kaufmann, 1975; Jordan and Ritchie, 1971; Kanemasu and Tanner, 1969). Differences in sensitivity between field and greenhouse grown plants of the same species suggested that there was a remarkable adaptation of stomatal apparatus to the growing condition.

The phenomenon of night-time stomatal opening seems to be the general rule in plants having the Crassulacean acid metabolism (CAM), and accounts for the 'inverted' pattern of gas exchange observed for these plants (Chen and Liaw, 1968; Neales, 1973; Neales et al., 1968; Nishida, 1968). This system of metabolism has

an adaptive significance and is usually described as conferring on plants the ability to grow in arid conditions (Evans, 1971; Neales et al., 1968; Pearcy et al., 1971; Ting, 1971). Night-time stomatal opening in a number of succulents was demonstrated using porometers (Nishida, 1963; Ting et al., 1967), a leaf cuvette (Neales et al., 1968), and from measurements of carbon dioxide assimilation (Joshi et al., 1965).

Succulents and xerophytes have been known to endure long periods of water stress. As such, small water deficits would not be expected to have any significant effect on these plant species. However, the stomata of plants having CAM also tend to close with increasing water stress, in a manner similar to mesophytic plants (Kluge and Fischer, 1967). Szarek et al. (1973) reported that during periods of high water stress, the transpiration rate of Opuntia basilaris, a desert cactus, was greatly reduced by stomatal closure. An important contribution of stomatal closure in this species was related to the ability of the plant to maintain a moderately active metabolic state by recycling endogenously produced carbon dioxide.

MATERIALS AND METHODS

1. EXPERIMENTAL DESIGN

Pineapple [*Ananas comosus* (L.) Merr. variety 'Smooth Cayenne'] crowns were collected at random from the Pineapple Research Institute field station, Wahiawa, Hawaii. The crowns were treated with Difolatan at 10 g l^{-1}, and cured by drying for three weeks. Planting was done in May, 1974 in approximately 6 kg Wahiawa soil packed in 15 cm wide by 35 cm deep black polyethylene bags. The soil was bulk fumigated with methyl bromide at the rate of 680 g m^{-1}. For stability, the filled bags were placed in plastic pots.

Preplanting fertilizers were applied at rates of 112 kg N as ammonium sulfate, 112 kg P_2O_5 as triple superphosphate, 168 kg K_2O as potassium sulfate, and 112 kg MgO as magnesium sulfate per hectare. Supplemental N as 5 percent urea solution and Fe as 1 percent ferrous sulfate solution were applied every three weeks by foliar spray. The plants were maintained with optimum water and pest control practices for about five months.

Treatments were imposed beginning October, 1974. The treatments consisted of a no-irrigation control and alternate cycles of wetting and drying to -1, -5, -10, and -15 bars. Each treatment was replicated 5 times and a replicate consisted of 5 plants. A randomized block design was used with each block on one of five separate benches in a glasshouse.

Soil moisture status was estimated by inserting thermocouple psychrometers (Wescor Instruments, Inc., PT 51-10) at about the mid-point of each plastic bag. Each psychrometer used was calibrated against 2 molal KCl prior to insertion into the soil. At the end of a drying cycle, the soil was brought to field capacity by watering the plants thoroughly once in the morning and once in the late afternoon.

A supplemental experiment consisting of no-irrigation control and the -1 bar treatment was conducted in the field at the Pineapple Research Institute, Wahiawa. Rainfall during the months of February, March and April prevented the manifestation of any treatment differences.

2. DATA COLLECTION

The effects of soil moisture status on pineapple were assessed by measuring leaf water potential and its components, relative water content, and leaf diffusion resistance. All measurements of plant water status utilized D-leaves (Krauss, 1948). The pineapple D-leaf is the youngest physiologically mature leaf. The D-leaf has been used to index plant nutrient levels, and evaluate effects of environment on plant moisture status and plant development, and D-leaf weight correlates highly with whole plant weight (Sanford, 1962).

The D-leaves used for measurement of leaf water potential and relative water content were brought to the laboratory in

tightly sealed plastic bags. Using sharp leaf punches, leaf discs 0.78 cm diameter were cut as rapidly as possible from the central portion of the leaf midway between the leaf base and tip. Fifteen leaf discs were cut from each leaf and a composite of discs from each treatment was made. The composited discs were stored temporarily in tightly capped vials.

Water status measurements were taken at the same time and date from all treatments by sampling when the soil water potentials of the various treatments were in phase. Light intensity was read with a lightmeter (Lambda Model L1 - 185, Lambda Instruments Co., Lincoln, Nebraska) and sensor (Lambda Model PY 259 - 7308).

The climate of the glasshouse was not controllable. Daytime temperatures in the glasshouse were reduced by the use of ventilator fans and an intermittent sprinkler system below the benches. Relative humidity and temperature were monitored throughout most of the experiment with a hygrothermograph (Model 594, Friez Instruments Division). Soil temperature was measured with thermocouples installed with the psychrometers.

Methods of measuring each parameter of plant water status under study are discussed in the following sections.

3. MEASUREMENTS OF LEAF WATER STATUS

3.1 Total Leaf Water Potential

The dye technique of Shardakow (1953), as modified by

Chapman (1970a), was used to estimate total leaf water potential. Mannitol solutions with osmotic potentials ranging from 1 to 26 bars in approximately 1-bar increments were prepared. Stock solutions were placed in plastic bottles and kept in the refrigerator to minimize microbial degradation. Tissue water potential was measured by placing 5 leaf discs from the composite sample mentioned previously into small vials containing about 5 ml of test solution. Each determination was replicated three times. The vials were stoppered and allowed to equilibrate for a predetermined period of time. After equilibration, the leaf discs were removed and discarded.

A control solution having the same osmotic potential as the test solution was prepared by mixing a small crystal of methylene blue with mannitol. A portion of the dyed solution was extracted with a dropper and carefully introduced into the test solution and the behavior of the drop was observed. The water potential of the leaf was taken to be equal to the concentration of the test solution if the control solution diffused into the test solution without moving vertically. Where the drop rose at one concentration and fell at the next, the water potential was then assumed to lie at some point between the two concentrations.

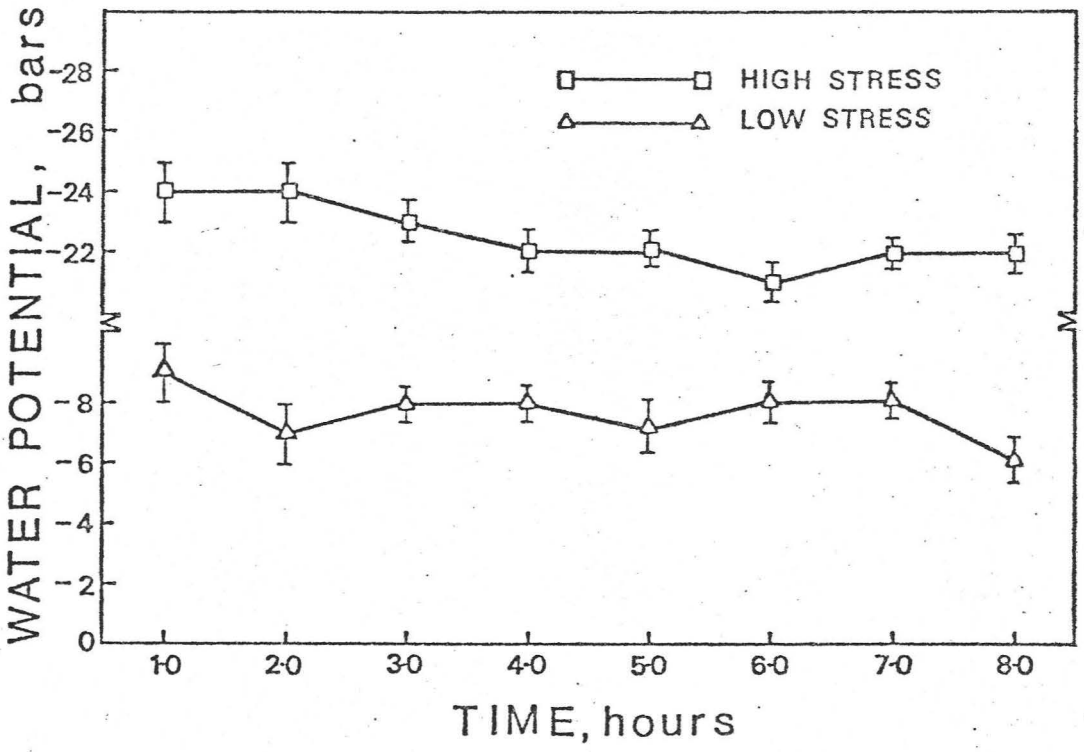
The effect of equilibration time on the water potential of pineapple discs was determined for low-stress and high-stress plants. Equilibration times up to 8 hours were examined.

The effect of equilibration time on total leaf water

potential was not significant for high or low stress plants (Figure 1). The results conflict with those of Wambiji (1972) who reported that a 6 hour equilibration time was inadequate for pineapple. The discrepancy between the results of Figure 1 and those of Wambiji (1972) may be due to the fact that Wambiji used sucrose rather than mannitol as the osmoticum. Barrs (1968) noted that sucrose is an unsatisfactory osmoticum for the determination of plant water potential because it is rapidly metabolized. The results were consistent with the work of others (Chapman, 1970a; Knipling, 1967) who found that 30 minutes was an adequate equilibration period for the determination of plant water potential by the Shardakov (1953) technique. For purposes of this study, a four hour equilibration time was selected on the basis of recommendations by Barrs (1968) that results generally are more consistent where tissues are equilibrated for a few to several hours. Also, although trends were not significant, leaf water potential of the stressed plants did not change after a four hour equilibration time (Figure 1).

The osmotic potential of leaf sap was measured with a WESCOR Model C-51 thermocouple psychrometer. Leaf discs from the composite sample were frozen in short lengths of 1.27 cm tygon tubing in a refrigerator at about -25 C. The tubes were then thawed at room temperature and the sap expressed at 227 kg m^{-2} pressure. The extracted sap was absorbed on filter paper discs. The well-soaked discs were then placed in the sample chamber and equilibrated

FIGURE 1. THE EFFECT OF EQUILIBRATION TIME ON THE TOTAL WATER POTENTIAL OF PINEAPPLE LEAF TISSUE FROM THE UNIRRIGATED CONTROL (□) AND THE -1 BAR (△) TREATMENTS. EACH POINT IS A MEAN OF 5 REPLICATIONS. VERTICAL LINES INDICATE STANDARD DEVIATIONS.


WATER POTENTIAL, bars
-28
-26
-24
-22
-8
-6
-4
-2
0
HIGH STRESS
LOW STRESS
1·0
2·0
3·0
4·0
5·0
6·0
7·0
8·0
TIME, hours

for 15 minutes. The osmotic potential was read from a calibration curve of microvolts versus solution osmotic potential. Sample chamber temperature was also measured with a copper-constantin thermocouple and osmotic potentials were corrected to 25 C.

Total leaf water potential is the algebraic sum of osmotic potential and turgor potential; matric potential was assumed to be zero (Equation 1). Turgor potential was, therefore, calculated as the difference between the total leaf water potential and osmotic potential. Because water potentials referenced to pure water are either zero or negative, there is the possibility of confusion occuring when referring to high and low values of water potential. To avoid possible confusion when comparing water potentials of the different treatments, a higher water potential refers to a less negative value while a lower water potential indicates a more negative value.

3.2 Relative Water Content

Relative water content was measured with a technique similar to that of Barrs and Weatherley (1962). Ten leaf discs were taken from a composite sample for the respective treatment and the fresh weight was taken on a precision balance. The discs were then floated in distilled water in vials. After a specified time had elapsed, the discs were removed, surface dried, and re-weighed. The leaf discs were subsequently oven-dried to a constant weight at about 75 C. Relative water content was calculated by

Equation 2.

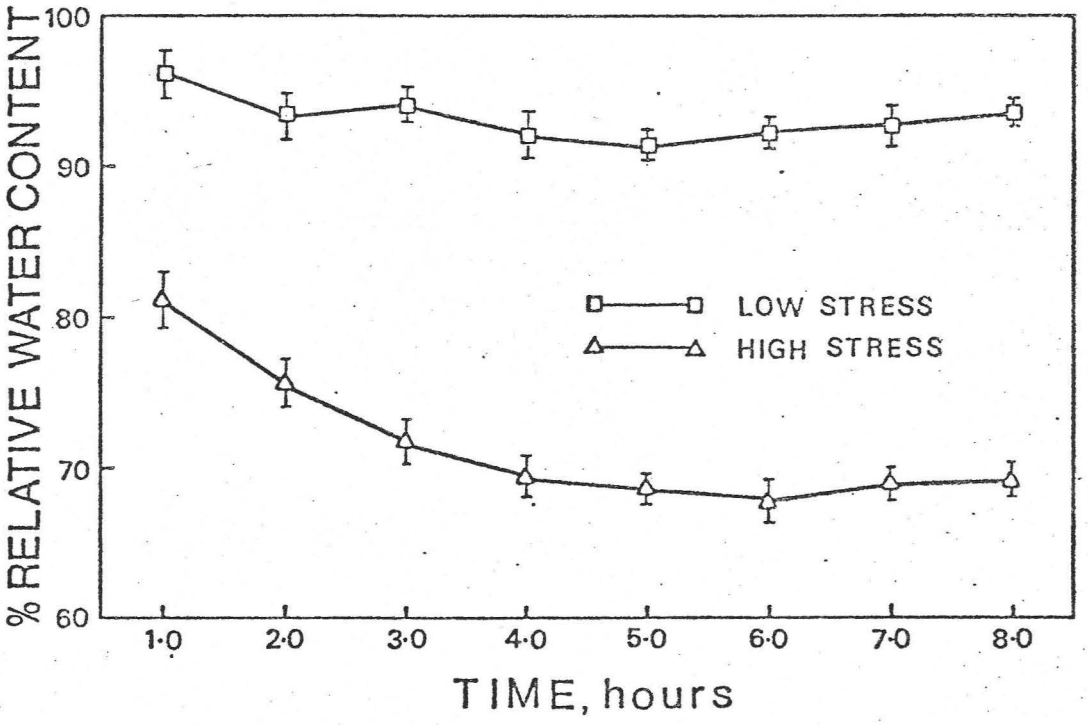
Equilibration time of leaf discs was determined for a low water stress (-1 bar) and a high water stress (unirrigated control) treatment. Five replicates were used at each equilibration time, and equilibration times of up to 8 hours were used (Figure 2). Initial uptake of water was more rapid in the unirrigated control than in the -1 bar treatment. The rate of water uptake tapered off with increasing time. The initial rapid uptake of water was similar to that reported by several workers (Barrs and Weatherley, 1962; Catsky, 1959; Chapman, 1973; Weatherley, 1950). The rapid uptake was postulated by Barrs and Weatherley (1962) and Chapman (1973) to be due to tissue water potential and the slow steady uptake was attributed to tissue growth.

On the basis of RWC data, a 4-hour equilibration time was chosen for all treatments. Other workers using the same technique have reported that equilibration time for leaf discs was in the neighborhood of 3 to 4 hours depending on the plant species (Barrs and Weatherley, 1962; Catsky, 1960).

3.3 Leaf Diffusion Resistance

Despite the development of various types of porometers, there is no commercial instrument suited for the measurement of leaf diffusion resistance of xerophytic plants such as pineapple. There was a need to develop an instrument which would estimate high leaf resistances with acceptable accuracy and be sufficiently

FIGURE 2. THE EFFECT OF EQUILIBRATION TIME ON RELATIVE WATER CONTENT OF PINEAPPLE LEAF TISSUE FROM THE UNIRRIGATED CONTROL (△) AND THE -1 BAR (□) TREATMENTS. EACH POINT IS A MEAN OF 5 REPLICATIONS. VERTICAL LINES INDICATE STANDARD DEVIATIONS.


% RELATIVE WATER CONTENT
100
90
80
70
60
LOW STRESS
HIGH STRESS
1·0
2·0
3·0
4·0
5·0
6·0
7·0
8·0
TIME, hours

sensitive to measure those resistances within 60 to 120 seconds.

Leaf diffusion resistance measurements of pineapple leaves were taken using a specially developed sensor cup, as described in the following sections. A diffusive resistance meter (Lambda Model L1-60, Lambda Instruments Co., Lincoln, Nebraska) was used to measure electrical resistance changes of the humidity sensor in the cup. All measurements of leaf resistance were made on the abaxial surface of D-leaves. Each leaf was shaded for a few minutes to minimize temperature differences between the leaf and the sensor cup.

3.3.1. The Porometer Cup Design

The leaf cup (Figure 3) was machined from a solid teflon block using a 15.88 mm round-end mill. Stigter et al. (1973) indicated that the choice of this material would essentially eliminate water vapor adsorption and desorption from the leaf cup walls. Cup dimensions were 1.588 cm wide, 1.588 cm deep, and 3.176 cm long, giving a cup aperture area of 4.499 cm^2. Cup volume, excluding the sensor, was 4.402 cm^3. The open end of the cup was covered with a perforated stainless steel plate (100 holes, 0.132 cm diameter, Figure 4) having 27% open area for protection of the sensor housed in the cup. The humidity sensor used was a miniature narrow range lithium chloride sensor (type H-7 part no. 15-1274) supplied commercially by Hygrodynamics Inc., Silverspring, Maryland. The sensor and the perforated plate were cemented in

FIGURE 3. CROSS-SECTION THROUGH THE SENSOR CUP.

1. Bead thermistor.
2. Perforated stainless steel plate.
3. Closed-cell foam rubber gasket.
4. Humidity sensor (Hygrodynamics Inc.).
5. Epoxy resin bonding sensor and cup.
6. Stainless steel tubing for entry of dry air from drying tube assembly.
7. Sensor cup.

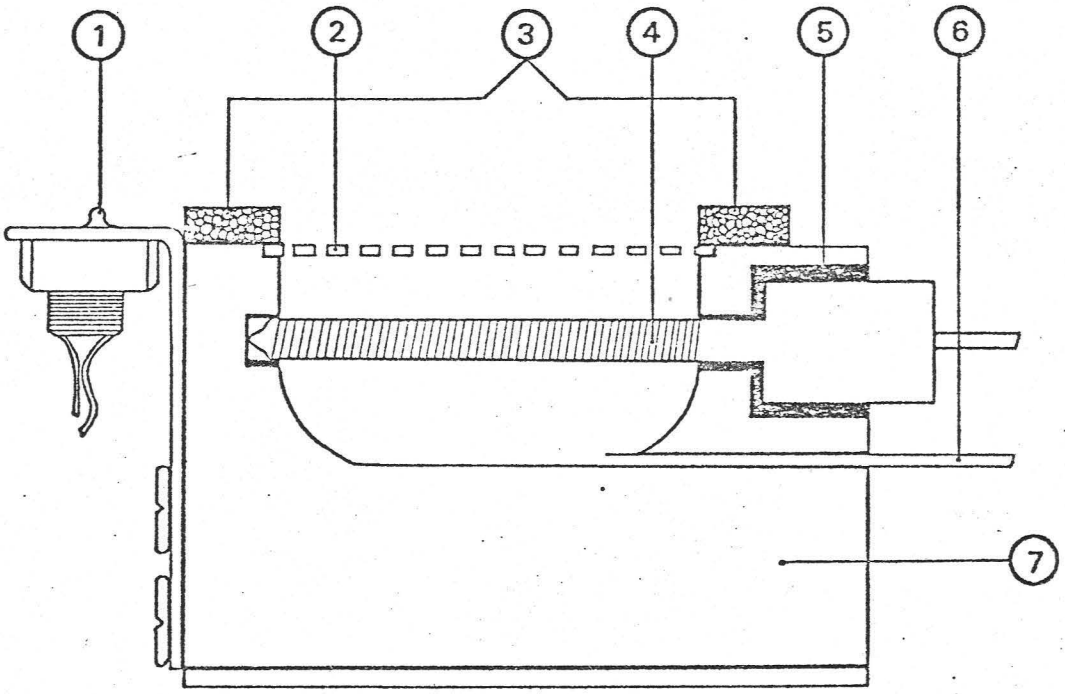
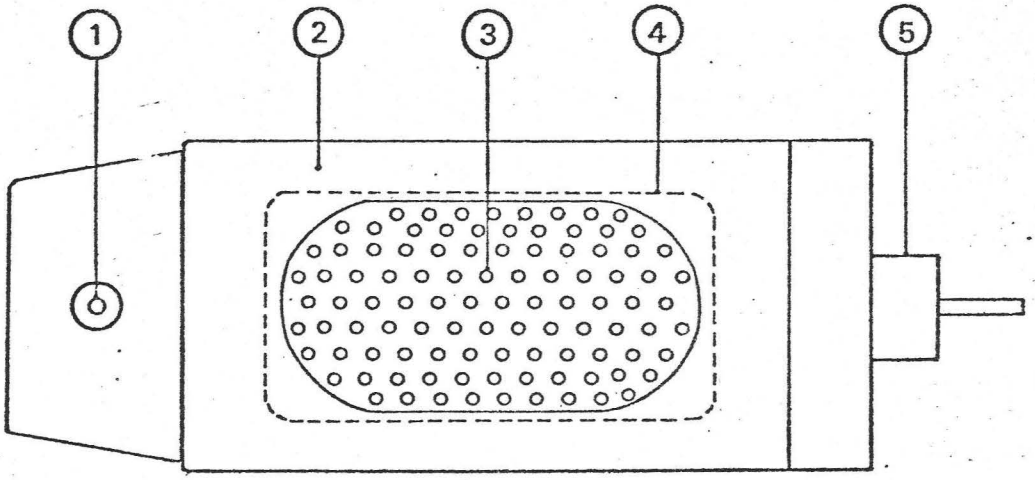

1
2
3
4
5
6
7

FIGURE 4. TOP VIEW OF SENSOR CUP.

1. Bead thermistor.
2. Closed-cell foam rubber gasket.
3. Holes (total of 100) for entry of water vapor.
4. Perforated stainless steel plate.
5. Sensor head.


1
2
3
4
5

place with a BA-500 epoxy adhesive after etching the teflon with Hi/D flurocarbon etchant No. 40 (Cadilac Plastic and Chemical Co.).

An air-tight seal with the leaf was obtained with a closed-cell foam rubber gasket (Self-adhesive foam refrigeration insulation tape, .32 cm thick). The teflon surface was etched before applying the foam gasket. A stainless steel tube was press-fit into the leaf cup chamber as a drying port. A bead thermistor was added to facilitate leaf temperature measurement. The position of the thermistor was adjustable (see Figure 3). The cup was mounted on an aluminium handle. The pressure of the cup against the leaf could be varied by a screw and nut (Figure 5). The whole unit was connected to a portable battery-operated resistance meter and silica gel drying assembly. When not is use the porometer cup was stored in a dessicator containing silica gel, as recommended by Stigter et al. (1973).

3.3.2. Calibration

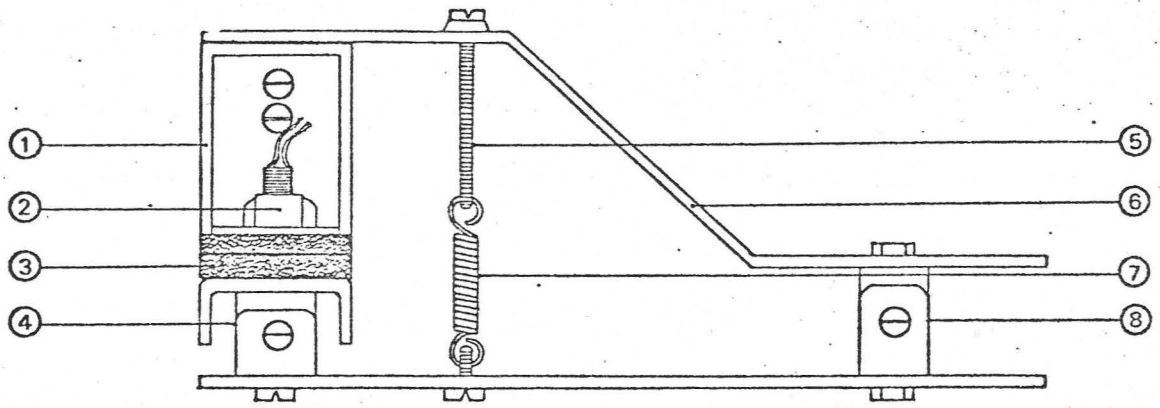
The sensor cup was calibrated by constructing an aluminium plate with 8 sets of holes having approximate water vapor diffusive resistance values of 2.5 6o 200 sec cm^{-1}. Resistances were computed by the following equation (Kanemasu et al., 1969):

$$r \text{ (sec cm}^{-1}) = 4A\ (L_o + \pi d/8)/\alpha n \pi d^2 \qquad (3)$$

where r = diffusive resistance to water vapor;

FIGURE 5. SIDE VIEW OF SENSOR CUP.

1. Sensor cup within which the humidity sensor is housed. The cup material is teflon (polytetrafluroethylene).
2. Bead thermistor.
3. Closed-cell foam rubber gasket.
4. Hinge.
5. Tension adjustment screw.
6. Aluminium handle.
7. Spring.
8. Hinge on handle.


1
2
3
4
5
6
7
8

α = diffusivity of water vapor at a given temperature;

A = aperture area of the sensor cup (4.499 cm^2);

L_o= actual thickness of each set of holes (0.648, 0.650, 0.658, 1.288, 1.293, 1.295, or 1.879 cm);

d = diameter of the hole in the calibration plate (0.118 cm);

n = number of holes per set (72, 34, 28, 20, 18, 14, or 13);

$\pi d/8$ = correlation factor.

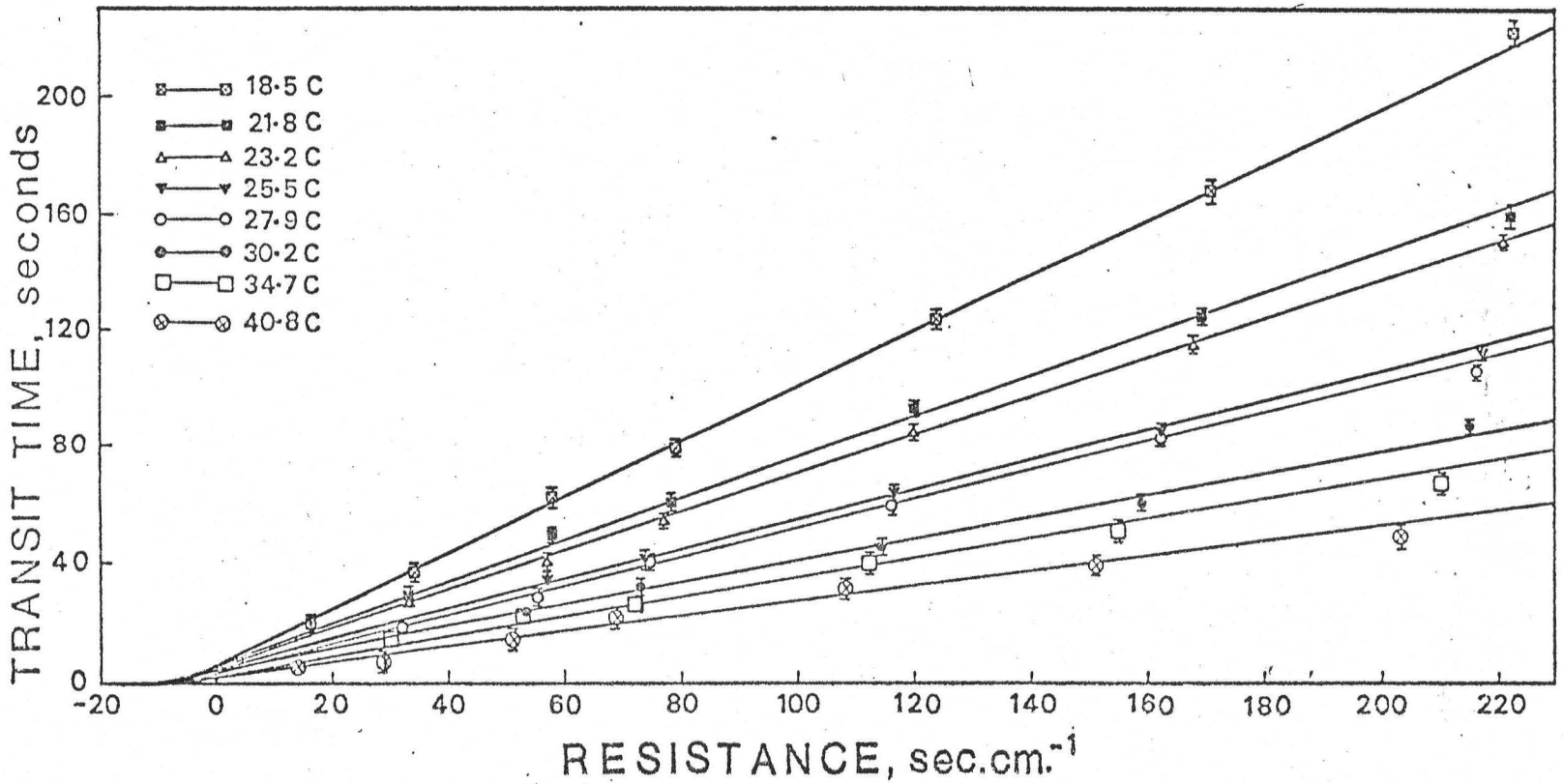
Before calibrating, the sensor cup was disassembled from the handle. The calibration plate was placed just above several layers of blotting paper saturated with deionized water. The cup was dried to a meter reading of 10 microamps on the H-1 sensitivity of the resistance meter by introducing dry air from the drying tube assembly. The cup was immediately and precisely placed on the plate over a set of holes. A 500 g weight was placed on the sensor cup to facilitate sealing of the cup to plate surface. Water vapor diffused through the holes in the plate to the porometer cup and the transit time (Δt) of the resistance meter from 20 to 60 microamps was obtained. The sensor was calibrated at temperatures ranging from 18 to 40 C. The calibrating temperature was determined by measuring blotting paper temperature with a calibrated thermocouple. All calibrations were performed in a temperature controlled chamber. Althrogh chamber humidity was not controllable, an attempt was made to maintain the relative humidity at about 70 percent.

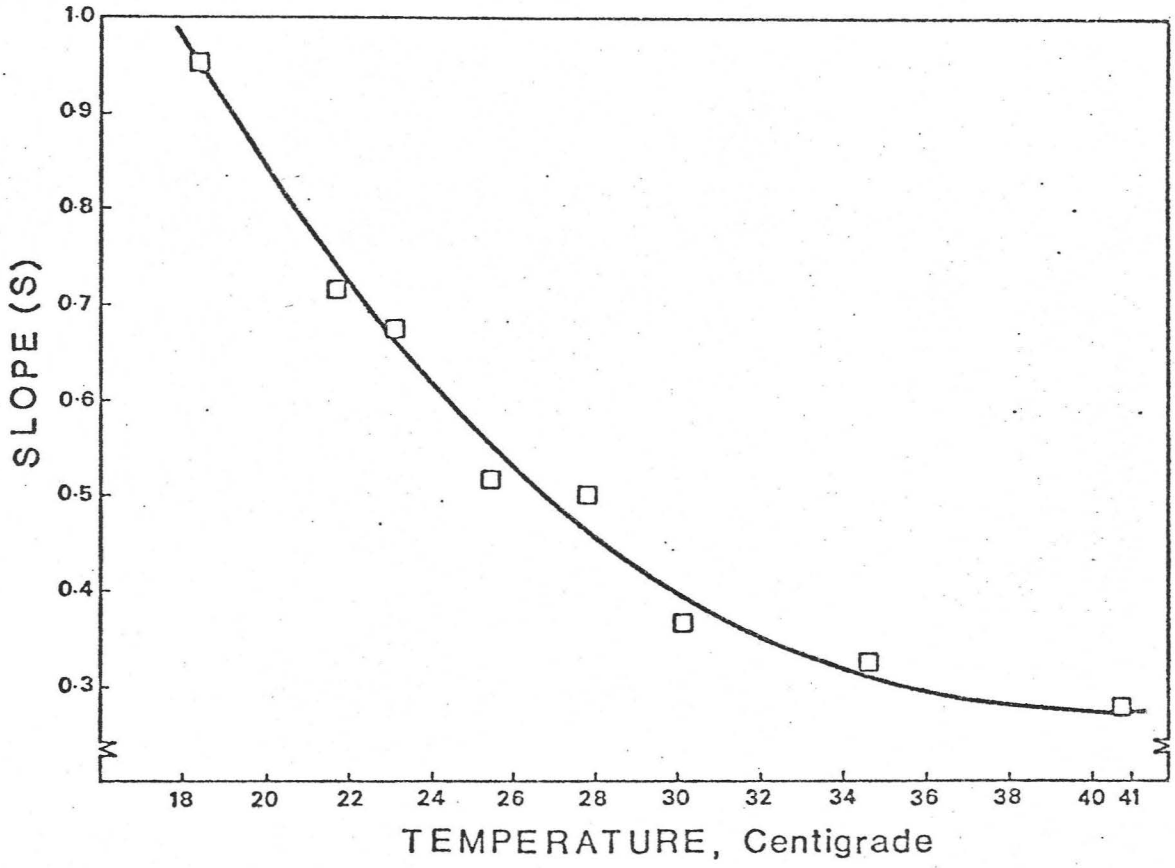
3.3.3. Instrument Test Results

A straight line relationship between transit time and calculated resistance in each calibrating temperature tested was obtained (Figure 6). A value of r_o, which is dependent upon cup and sensor geometry, was obtained by extrapolating the calibration curves (Figure 6) to y = 0. The average value for r_o was -6.824. The data parallel the findings of others, but extend the calibration curves an order of magnitude beyond those reported (Kanemasu et al., 1969; Meidner, 1970; Morrow and Slatyer, 1971; Stigter et al., 1973; Turner and Parlange, 1970; van Bavel et al., 1965). The relationship between resistance and transit time appeared to depart from linearity at resistances higher than 200 sec cm^{-1}. Regression equations were calculated on the basis of resistances below 200 sec cm^{-1}. Although the apparent lack of linearity may be due to leakage of air from outside the sensor through the gasket, no further attempt was made to investigate the source of error.

By plotting the slopes of the calibration curves against temperature, a curve was obtained from which the slope or sensitivity (S) for any temperature could be approximated (Figure 7). From a measurement of Δt in the field and using the appropriate S, leaf resistance values were calculated by the equation of Kanemasu et al. (1969) :

$$r_l = r_o + \Delta t/S$$


18·5 C
21·8 C
23·2 C
25·5 C
27·9 C
30·2 C
34·7 C
40·8 C
TRANSIT TIME, seconds
0
40
80
120
160
200
-20
0
20
40
60
80
100
120
140
160
180
200
220
RESISTANCE, sec.cm.-1


1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
SLOPE (S)
18
20
22
24
26
28
30
32
34
36
38
40
41
TEMPERATURE, Centigrade

where r_l is leaf diffusive resistance, r_o is the resistance of the porometer cup; Δt is the transit time, and S is the sensitivity at the leaf temperature.

RESULTS AND DISCUSSION

Measurements of total leaf water potential, osmotic potential, relative water content, and leaf diffusion resistance to water vapor transfer were made under conditions of varying soil water potential. Unless otherwise stated, all observations were made on clear days. Measurements of temperature and relative humidity were made during most of the test period from February to May, 1975 and are shown in Tables I and II. All parameters of plant-soil-water status measured are discussed in the following sections.

SOIL WATER POTENTIAL

The number of days required to reach a given soil water potential are shown in Figure 8. The moisture level for the -1 bar treatment was the most difficult to measure accurately. The approximate level was first reached about 7 days after the treatments were imposed. The -5 bar stress level was reached in 13 to 14 days after irrigation. The -10 and -15 bar levels were reached about 19 and 25 days respectively after each irrigation. In the control, soil moisture tension continued to become more negative with time.

When all treatments, except the control, reached their predetermined levels of stress at the same time, irrigation was withheld and measurements of leaf resistance and plant water status were made. After these measurements, all plants were irrigated to

TABLE I

WEEKLY AVERAGE TEMPERATURE IN THE GREENHOUSE DURING TEST PERIOD FROM FEBRUARY TO MAY, 1975

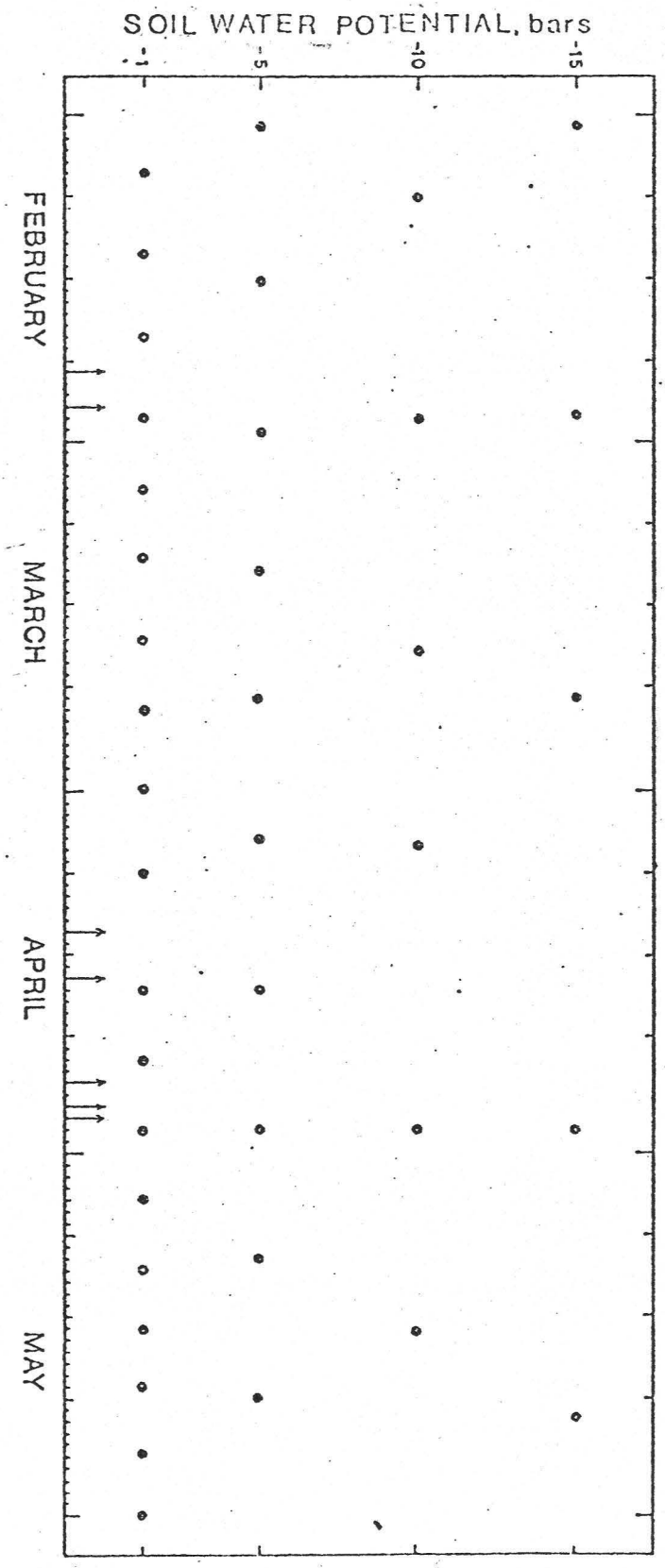
	TEMPERATURE, C (MINIMUM - MAXIMUM)			
WEEK	FEBRUARY	MARCH	APRIL	MAY
1	23.0 - 34.0	22.2 - 36.7	24.0 - 36.0	27.0 - 38.0
2	...	...	...	25.0 - 38.0
3	21.8 - 33.7	...	25.7 - 37.0	...
4	20.2 - 33.3	23.5 - 34.0	23.8 - 36.0	26.8 - 39.0

TABLE II

WEEKLY AVERAGE RELATIVE HUMIDITY IN THE GREENHOUSE DURING TEST PERIOD FROM FEBRUARY TO MAY, 1975

	RELATIVE HUMIDITY, PERCENT (MINIMUM - MAXIMUM)			
WEEK	FEBRUARY	MARCH	APRIL	MAY
1	40.0 - 88.0	...	...	...
2	35.0 - 92.0	30.0 - 92.0	30.0 - 90.0	...
3	38.0 - 96.0	33.0 - 96.0	...	30.0 - 96.0
4	...	...	...	...

FIGURE 8. IRRIGATION FREQUENCY FOR THE -1, -5, -10, AND -15 BAR TREATMENTS BETWEEN FEBRUARY AND MAY, 1975. EACH DOT REPRESENTS ONE IRRIGATION. ARROWS INDICATE MEASUREMENTS OF PLANT WATER STATUS.


SOIL WATER POTENTIAL, bars
-1
-5
-10
-15
FEBRUARY
MARCH
APRIL
MAY

field capacity and allowed to dry again. Approximately 2 months later, the control treatment was also irrigated to field capacity merely to allow the continuation of plant growth. Soil water content throughout the profile taken from one plant from each treatment was consistently uniform (Table III). Apparently, water extraction by the plant proceeded sufficiently slowly so that water content gradients in the soil profile were minimized.

TABLE III

GRAVIMETRIC SOIL WATER CONTENT ALONG THE PROFILE AT SEVERAL SOIL WATER POTENTIALS. EACH VALUE IS A MEAN OF 3 SAMPLES WHICH WERE MEASURED ON APRIL 27

SOIL WATER POTENTIAL (BAR)	SOIL WATER CONTENT (PERCENT) TOP	MIDDLE	BOTTOM
- 1	46.8	47.0	47.0
- 5	31.3	31.4	31.6
-10	25.4	25.4	25.6
-15	24.4	25.0	25.4
-21	13.3	13.4	14.0

No soil water status measurements were made in the field as rainfall was adequate to maintain the soil at or near field capacity.

PLANT GROWTH

The first measurable effect of water stress in plants if often demonstrated by a reduction of growth and development. Table IV shows the total dry weight of pineapple plants after seven months of growth at five soil moisture levels (a total of 12 months growth).

Plant growth was affected significantly by water supply. However, the plants were very small when compared with field grown plants which attain about 500 g dry weight after one-years growth (Bartholomew, personal communication). High greenhouse temperatures and inadequate nutrition are two possible reasons for the poor growth. Greenhouse air temperatures exceeded the 32 C optimum for leaf growth (Sanford, 1962) by several degrees (Table I) and the temperature of sunlit leaves can be 10 C or more above air temperature (Aubert and Bartholomew, 1973). Soil temperature obtained in the afternoon on several occasions (Table V) apparently did not exceed the 29 C optimum temperature for root growth (Sanford, 1962). Mineral nutrient analysis of D-leaves of several plants showed phosphorus to be below the critical level required for normal growth.

Water stress also affected plant composition. However, statistical analyses of the differences could not be made. Roots, stems and leaves were weighed separately but the parts of individual plants were not identified so the variation in percent composition at a given level of treatment could not be obtained.

TABLE IV

DRY WEIGHT OF PINEAPPLE PLANTS AFTER 7 MONTHS GROWTH AT 5 SOIL MOISTURE LEVELS
EACH VALUE IS A MEAN OF 15 PLANTS*

TREATMENT		STEM WEIGHT (g)	STEM % MEAN TOTAL	ROOT WEIGHT (g)	ROOT % MEAN TOTAL	LEAF WEIGHT (g)	LEAF % MEAN TOTAL	TOTAL WEIGHT (g)
	MIN.	20.6	13.1	19.7	12.5	108.7	69.2	
- 1 BAR	MAX.	25.4	16.2	25.6	16.3	115.2	73.4	
	MEAN	23.5[a]	15.0	22.0[a]	14.0	111.5[a]	71.0	157.0
	MIN.	19.2	12.8	18.8	12.5	105.1	70.0	
- 5 BARS	MAX.	23.4	15.6	22.6	15.0	110.8	73.8	
	MEAN	21.8[a]	14.5	20.9[a]	13.9	107.5[a]	71.6	150.2
-10 BARS	MIN.	19.7	17.3	16.3	14.3	69.7	61.4	
	MAX.	24.8	21.8	21.5	18.9	76.3	67.2	
	MEAN	20.7[b]	18.2	18.0[a]	15.8	74.9[b]	66.0	113.6
	MIN.	17.4	16.4	10.7	10.1	70.6	66.7	
-15 BARS	MAX.	22.5	21.3	14.1	13.3	75.8	71.6	
	MEAN	19.9[b]	18.8	12.4[b]	11.7	73.5[b]	69.5	105.8
	MIN.	14.3	17.2	6.8	8.2	55.1	66.1	
CONTROL	MAX.	17.8	21.4	9.2	11.0	62.3	74.8	
	MEAN	16.0[b]	19.2	7.6[b]	9.1	59.7[c]	71.7	83.3

* Values followed by a common letter are not significantly different.

TABLE V

SOIL TEMPERATURES OF THE
-1 AND -5 BAR TREATMENTS IN THE GREENHOUSE
EACH VALUE IS A MEAN OF 3 OBSERVATIONS

DATE	-1 BAR	-5 BARS	DATE	-1 BAR	-5 BARS
2/01	...	27	3/23	28	...
2/05	27	...	3/30	28	...
2/12	27	...	4/04	...	29
2/14	...	27	4/07	29	...
2/19	27	...	4/17	29	28
2/26	27	...	4/23	...	28
2/27	...	28	4/29	28	28
3/04	28	...	5/04	29	...
3/10	27	...	5/09	...	29
3/11	...	28	5/10	28	...
3/22	...	28	5/15	28	28

In lieu of this, the range in percent of stem for a given treatment was calculated by dividing the mean total plant weight into the largest and smallest stem weights. If ranges for the different treatments did not overlap, it was considered probable that percent composition differences were real. The range of values for stem as a percentage of total weight at -1 and -5 bar treatments was from 12.8% to 16.2% while the range for the other treatments was 16.4% to 21.4%. The absence of overlap with the two high-water treatments suggests a real difference in percentage of stem due to treatment. By a similar analysis, root weights of the unirrigated control, as a percent of total weight, (range of 8.2 to 11.0%) did not overlap root weight percentages for the -1, -5 and -10 bar

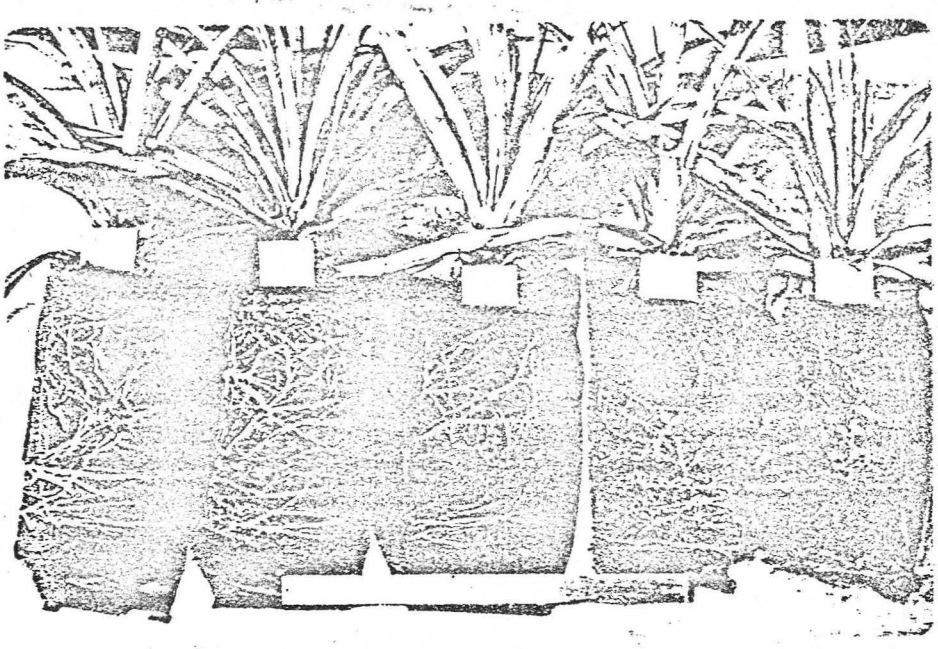
treatments (range of 12.5 to 18.9%) and were, therefore, considered to be different. Percentage of roots at -15 bars was intermediate between those for the high and low moisture treatments.

The general reduction in the total dry weight with increasing stress could be due to direct and indirect effects of water deficit on physiological processes. A reduction in growth could be caused by reduced cell enlargement. Boyer (1970a) reported that cell enlargement was inhibited by a decrease in turgor caused by a water deficit. Much of the reduction in growth and development of water stressed pineapple plants could also be due to a reduction in photosynthesis, caused by stomatal closure which reduced carbon dioxide uptake.

Visual examination of root distribution in each treatment showed that the majority of the roots were localized between the soil and the plastic bag in the lower 20 cm of each profile (Figure 9). The effects of stresses on root development are also apparent in Figure 10. Although root development was reduced with increasing water stress, root elongation tended to be somewhat similar (Figure 10) with maximum lengths not exceeding 35 cm. Little is known of the effects of water stress on root development. The general decrease in root weight with increasing stress (Table IV) is probably due to a reduction in meristematic activity associated with internal water deficit. Ekern (1967) cited an unpublished work that showed the critical level of soil water

FIGURE 9. ROOT GROWTH AND DISTRIBUTION AMONG 5 TREATMENTS. FROM LEFT TO RIGHT : -1 BAR, -5 BARS, -10 BARS, -15 BARS, AND UNIRRIGATED CONTROL.

FIGURE 10. ROOT ELONGATION AT 5 SOIL MOISTURE LEVELS. FROM RIGHT TO LEFT : -1 BAR, -5 BARS, -10 BARS, -15 BARS, AND UNIRRIGATED CONTROL.



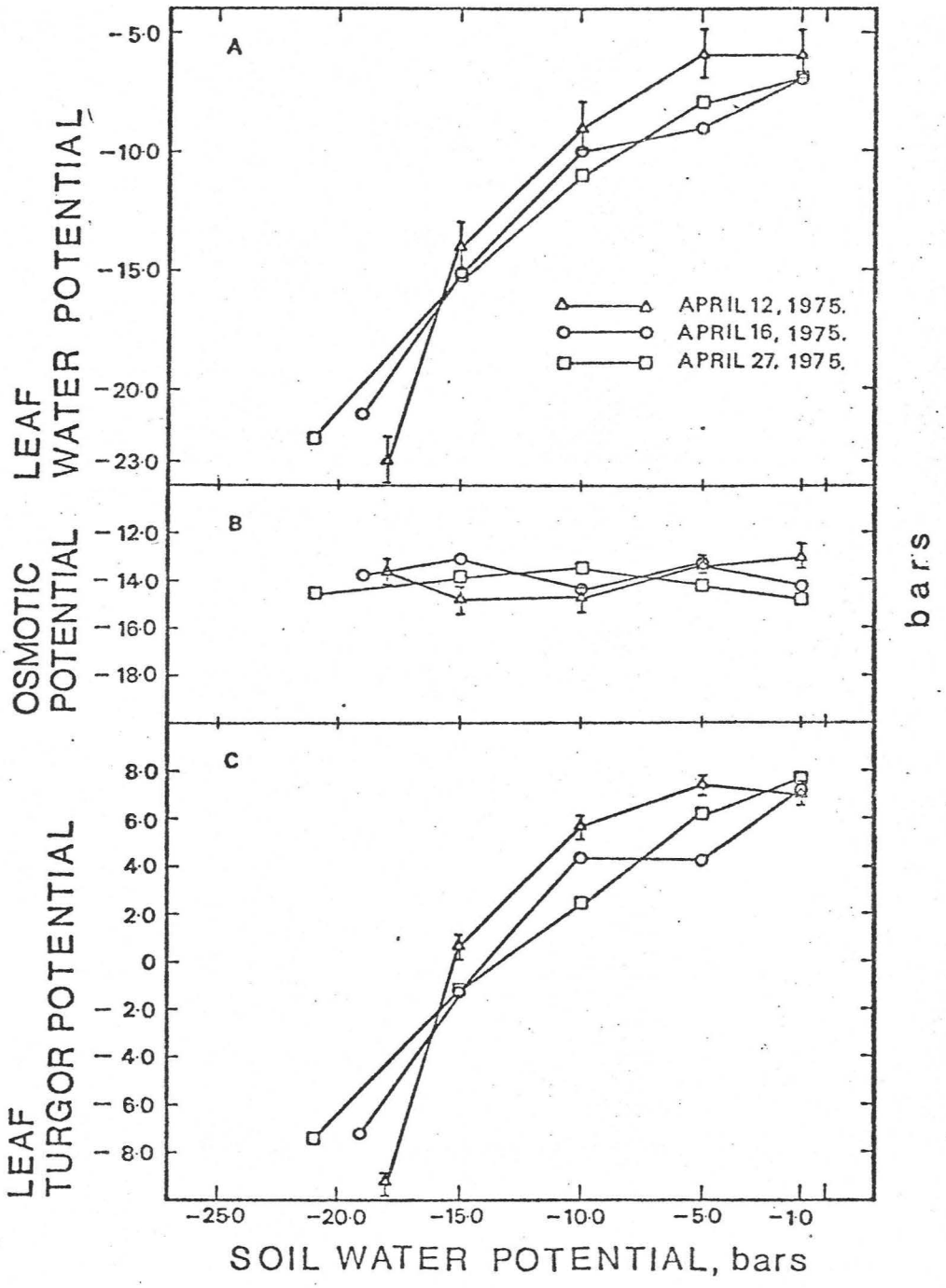
potential for root growth of pineapple was -15 bars. When the soil reached this level of stress, root elongation ceased and root tips underwent suberization.

EFFECTS OF SOIL WATER POTENTIAL ON LEAF WATER POTENTIAL

Simultaneous measurements of soil water potential, leaf water potential and osmotic potential were made on April 12, 16 and 27. Soil water potentials ranged from -1 to -18 bars on April 12. The soil water potential of all treatments, except the unirrigated control, remained unchanged from April 12 to April 27. The -1 and -5 bar treatments were irrigated once during the period of measurement. A low soil water content associated with limited water extraction from the soil by plants at the higher levels of stress may account for the lack of change in the -10 and -15 bar treatments. The reason for the decrease in soil water potential for the unirrigated control from -18 to -21 bars over the period from April 12 to April 27 is not obvious but could be due to the fact that in nearly dry soil, the loss of very small amounts of water would result in large increases in soil water potential.

Data for total water potential, osmotic potential, and turgor potential of pineapple leaves measured on the three occasions are presented in Figure 11. Leaf tissues were sampled between 1000 and 1100 hours when leaf resistance was near maximum. On the three occasions, leaf water potential became more negative with decreasing soil moisture. On April 12, the highest leaf water

FIGURE 11. THE INFLUENCE OF SOIL WATER POTENTIAL ON TOTAL LEAF WATER POTENTIAL (A), OSMOTIC POTENTIAL (B), AND TURGOR POTENTIAL (C) OF PINEAPPLE ON APRIL 12, APRIL 16, AND APRIL 27, 1975. VERTICAL LINES INDICATE STANDARD DEVIATIONS.


A
B
C
LEAF WATER POTENTIAL
OSMOTIC POTENTIAL
LEAF TURGOR POTENTIAL
bars
-5·0
-10·0
-15·0
-20·0
-23·0
-12·0
-14·0
-16·0
-18·0
8·0
6·0
4·0
2·0
0
- 2·0
- 4·0
- 6·0
- 8·0
APRIL 12, 1975.
APRIL 16, 1975.
APRIL 27, 1975.
-25·0
-20·0
-15·0
-10·0
-5·0
-1·0
SOIL WATER POTENTIAL, bars

potential value reached in the -1 bar treatment was -6 bars. The lowest water potential value attained in the unirrigated control plants was approximately -23 bars and the soil water potential was about -18 bars. On April 16 and 27, the soil water potential of the unirrigated control dropped further to -19 and -21 bars respectively. Total leaf water potential on those occasions was approximately -21 bars for the former and -22 bars for the latter.

Other estimates of leaf water potential for pineapple using the dye technique (Bartholomew, unpublished) indicated that normal values for pineapple plants ranged from -4 to -8 bars. Water potential was found to decrease from -4 to -5 bars at the base to -7 to -8 bars at the tip of the leaf. Wambiji and El-Swaify (1974) studied the effects of soil salinity on pineapple leaf water potential and growth. They reported that leaf water potential decreased linearly as salinity level increased. The lowest values of leaf water potential were of the order of -20 to -30 bars. In contrast to the data of Wambiji and El-Swaify (1974), the leaf water potential of pineapple exposed to matric stress decreased curvilinearly with decreasing soil water potential (Figure 11). Wambiji and El-Swaify (1974) attirbuted the linear response as adjustment of the plant to changes in osmotic potential in the soil solution.

The lack of similarity between our data and those of

Wambiji and El-Swaify (1974) presumably could be due to the types of stress to which the plants were exposed. The data of Gingrich and Russell (1957) support this contention. They reported that radicle elongation and increase in fresh weight of corn seedlings as a function of soil moisture tension were non-linear, but growth was linearly related to osmotic stress at least between -0.3 to -12 bars. They attributed the different relationships to a decrease in the rate of water movement in soil with decreasing water content while in solution cultures, root permeability and water supply would tend to remain more nearly constant.

The magnitude of change in leaf sap osmotic potential with changes in soil water potential was determined with a Wescor thermocouple psychrometer. Leaf sap extracted from frozen discs was placed in the sample chamber of the psychrometer and allowed to equilibrate for about 15 minutes. Osmotic potential did not change significantly with changes in soil water potential and values were consistently in the range of about -13 to -15 bars (Figure 11). These values were lower than the leaf water potential in the -1, -5 and -10 bar treatments, but in the -15 bar treatment and the unirrigated control plants the osmotic potential was generally higher than the leaf water potential. The results show that for pineapple grown in soil, osmotic potential would not be a sensitive indicator of leaf water deficit, at least within the range of water stress tested in this study.

The lack of a change in osmotic potential with such a

large change in total water potential is somewhat surprising. The osmotic potential of corn decreased from -9.6 to -13.4 bars in irrigated and dry soil respectively, and demonstrated that osmotic adjustment to matric stress occurred in this mesophyte. The reason for this lack of change is not evident from the data obtained. However, if the presence of hydrophilic substances in the water storage tissue results in a matric potential which balances osmotic and matric forces in adjacent mesophyll cells, total plant water potential and relative water content could decrease without any appreciable change occurring in osmotic potential. In such a system, water lost from mesophyll cells would be replenished by water in the water-storage tissue. Osmotic potential would thus remain relatively unchanged while total leaf water potential and RWC decreased due to decreased turgor and matric potentials of cells in the water-storage tissue.

Turgor potentials (Figure 11), calculated as the difference between leaf water potential and osmotic potential (Equation 1), in the -1 bar treatment were about +7 bars. The results are in agreement with those of other workers who indicated that the turgor potential of well-watered leaves may be of the order of +5 to +9 bars (Barrs, 1968; Boyer, 1968; Gardner and Ehlig, 1965: Kanemasu and Tanner, 1969). In the unirrigated control where leaf water potential was at -23 bars, turgor potential was as low as -9 bars. Negative turgor could arise as a result of increased

tension between the protoplast and the cell wall (Slatyer, 1960), as a result of a more negative matric component due to the loss of water from the cell (Boyer, 1967b) or both. It is also possible that negative turgor values were an artifact of the measurement technique; however, the regular decrease in turgor potential with decreasing soil water potential would argue against that possibility.

Negative turgor potential values have been reported by a number of workers. Noy-Meir and Ginzburg (1969) indicated that xerophytic plants like Atriplex halimus developed relatively large negative turgor potentials as soil water potential declined. Boyer (1965), Ehlig (1962), and Gavande and Taylor (1967) found small negative turgor potentials for a number of plant species with the wet-loop thermocouple psychrometer technique. Turner (1974) also observed negative turgor potentials of up to -5 bars in the leaves of maize, sorghum and tobacco. While negative turgor potentials have been reported for a number of plants, Boyer (1967b) appears to be one of the few workers who attempted to measure matric potential directly and thus, to provide more direct evidence for the presence or absence of negative turgor. Noy-Meir and Ginzburg (1969) found that the rank of drought tolerance, as measured by the water potential at maximum negative turgor, was the same as the rank of aridity in natural habits for several species. The gradual increase in the negative turgor potential component in pineapple with decreasing soil water

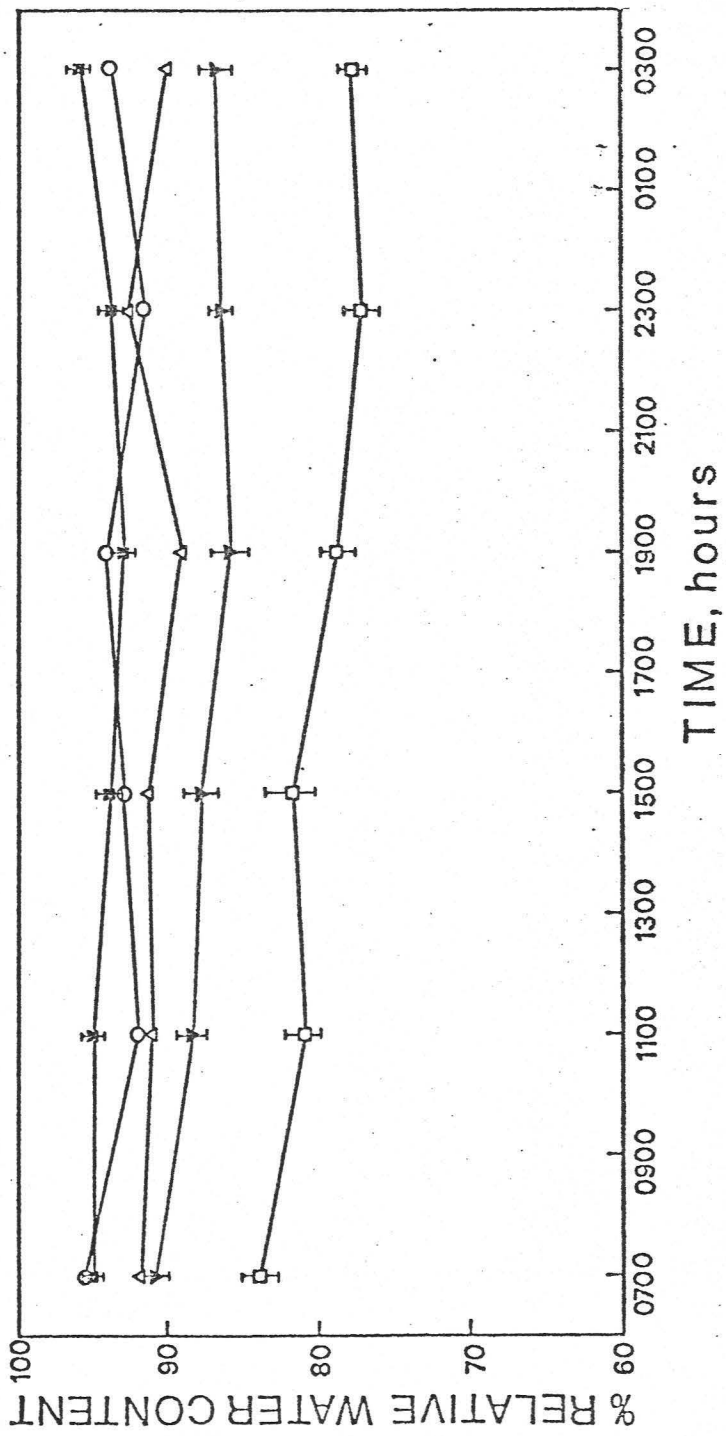
potential may, therefore, reinforce this observation. However, the possibility that negative turgor is in fact a decrease in the matric component cannot be ruled out.

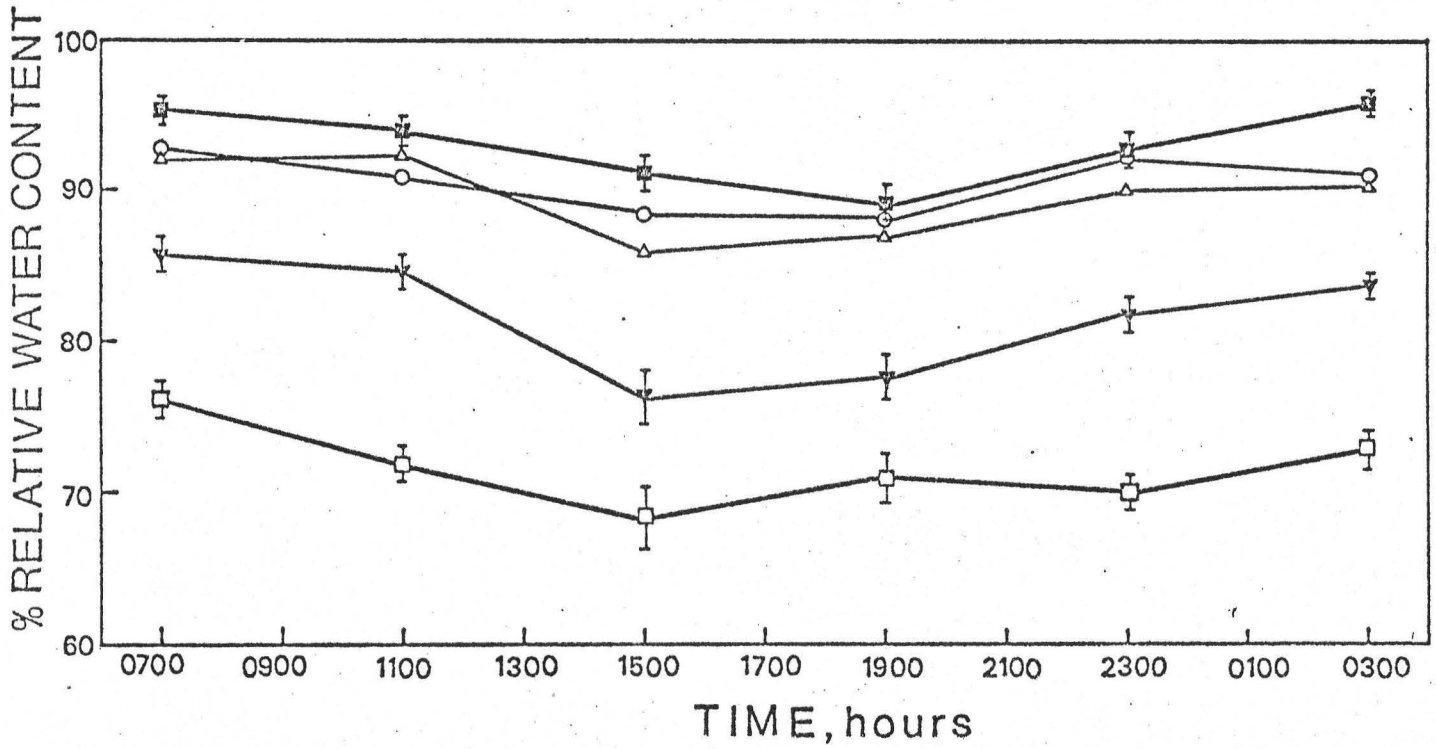
EFFECT OF SOIL WATER POTENTIAL ON RELATIVE WATER CONTENT

The diurnal trend of RWC was measured on three occasions. Two sets of measurements are shown in Figure 12 and Figure 13. Relative water content was lower during the afternoon hours than at sunrise but was significant only for the April measurements (Figure 13, Table XIV). There was a general decrease in RWC with a decrease in soil moisture status. Relative water content of the unirrigated control plants ranged from maximums of 84 and 76 percent at 0700 hours to minimums of 78 and 69 percent (Figure 12 and Figure 13 respectively). Water deficits were in the leaves at all times of the day. The RWC of the plants maintained at -1 bar did not reach 100 percent at any time of the day. The highest value attained was about 96 percent at 0300 hours.

The progressive decrease in RWC which accompanied increases in soil moisture stress have also been reported by various workers (Ehlig and Gardner, 1964; Jarvis and Jarvis, 1963; Slatyer, 1957; Weatherley and Slatyer, 1957). Slatyer (1960) showed that at a soil water potential of -20 bars, RWC was about 50 percent in tomato leaves and 90 percent in the phyllodes of the xerophyte Acacia aneura. At a soil water potential of about -21 bars, the RWC for the unirrigated control pineapple plant (Figure 13) was intermediate between that of tomato and Acacia

FIGURE 12. DIURNAL TRENDS OF RELATIVE WATER CONTENT IN PINEAPPLE AT 5 LEVELS OF STRESS MEASURED ON FEBRUARY 25 AND 26, 1975. EACH OBSERVATION IS A MEAN OF 5 REPLICATIONS. THE TREATMENTS CONSIST OF UNIRRIGATED CONTROL (□), AND IRRIGATION AT -1 (▣), -5 (○), -10 (△), AND -15 (▽) BARS. VERTICAL LINES INDICATE STANDARD DEVIATIONS.


% RELATIVE WATER CONTENT
100
90
80
70
60
0700
0900
1100
1300
1500
1700
1900
2100
2300
0100
0300
TIME, hours


% RELATIVE WATER CONTENT
100
90
80
70
60
0700
0900
1100
1300
1500
1700
1900
2100
2300
0100
0300
TIME, hours

aneura (Slatyer, 1960).

The fact that RWC never reached 100 percent, at least on the days when the measurements were taken, suggests that water deficits developed during the day were not replenished adequately during the night. Similar observations have also been reported by Weatherley (1951) for cotton. Downey and Miller (1971) indicated that in most field trials, the range of RWC of greatest importance was between 88 and 99 percent. Values below 83 percent were seldom observed except in cases where plants were dessicated.

Downey and Miller (1971) also indicated that a corn leaf showed visible wilting at about 86 percent RWC. In pineapple, visible wilting of leaves was not apparent even at RWC of 69 percent. This is presumably due to the relatively rigid leaves which are well-supported by veins and fiber bundles. Sanford (personal communication) indicated that the crescent-shaped leaf of the pineapple offers about 50 times more resistance to bending than any leaf with a flat blade having the same surface area and thickness.

Another striking difference between corn and pineapple is that of transpiration rate. Ehrler (1969) reported that corn followed the conventional pattern of transpiration, and being closely related to the evaporative demand, it attained a high rate of loss of water per unit leaf area. Transpiration from pineapple is about one tenth the rate of maize (Ekern, 1965; Neales et al.,

1968; Yoder, 1969) and evapotranspiration in the field was not closely coupled to the environmental demand (Ekern, 1965). Published leaf diffusive resistance data (Aubert, 1971) also showed that field grown pineapple could be expected to have low transpiration rates during the day. Downey and Miller (1971) indicated that the upper and lower limit of RWC of maize is set, at least in part, by the rate of transpiration. Thus, in pineapple, with the rate of transpiration being low and essentially independent of daytime evaporative demand, RWC tends to remain somewhat constant and visual wilting does no develop until water deficits in the leaves are extremely high.

The water-storage tissue in pineapple is a striking feature of the plant, and comprises one-fourth to two-thirds of the leaf cross-section (Krauss, 1949). In a fully developed turgid pineapple leaf, water-storage tissue occupies approximately one-half the cross-section of the leaf. Sanford (1962) indicated that the relative thickness of water-storage tissues of pineapple D-leaves could be used to index plant water deficits.

Quantitative relationships between leaf thickness and RWC or leaf water potential were not made for pineapple in this study. However, there were indications of reduced stiffness of the leaf blades of plants grown at high levels of stress. Gardner and Ehlig (1965) found that changes in leaf thickness of pepper, sunflower and birdsfoot trefoil were related to turgor pressure but the amount of leaf shrinkage varied among the species. As leaves of

pineapple were relatively rigid and well-supported by veins (Krauss, 1949) they could only exhibit modest wilting symptoms.

The relationships between water stress and total leaf water potential, turgor potential, and RWC are shown in Table VI. Here, we assumed that no significant changes in water potential or RWC occurred within the 24-hour period between measurements. Relative water content decreased with decreasing soil moisture and changes approximately paralleled changes in turgor potential and total water potential. Similar results have also been obtained by Connor and Tunstall (1968) and Millar et al. (1968).

TABLE VI

RELATIONSHIPS BETWEEN WATER STRESS AND TOTAL LEAF WATER POTENTIAL, OSMOTIC POTENTIAL, TURGOR POTENTIAL, AND RELATIVE WATER CONTENT OF PINEAPPLE

SOIL WATER POTENTIAL (BARS)	LEAF WATER POTENTIAL* (BARS)	OSMOTIC POTENTIAL* (BARS)	TURGOR POTENTIAL* (BARS)	RELATIVE WATER CONTENT** (PERCENT)
- 1	- 7	-14.83	+7.83	94.13
- 5	- 8	-14.16	+6.16	91.23
-10	-11	-13.53	+2.53	92.19
-15	-15	-13.83	-1.17	84.66
-21	-22	-14.60	-7.40	72.23

* Data from Figure 11, taken on April 27 at 1100 hours.

** Data from Figure 13, taken on April 28 at 1100 hours.

The response of the plants to decreasing soil moisture,

in terms of leaf water potential, turgor potential, and RWC, is of particular interest. The RWC-water stress relationship has practical significance as the degree of turgidity at any one level of stress is indicative of the physiological activity of the plant. As dehydration proceeds beyond the state such that there is zero turgor potential, the water in the cells passes into a state of tension and cells in the water-storage tissue would begin to collapse. Negative turgor then develops resulting in inward folding of the cell walls. The inward curling of leaf margins observed in the unirrigated control plants was probably indicative of this phenomenon.

EFFECTS OF SOIL WATER POTENTIAL ON LEAF DIFFUSION RESISTANCE

The development of a porometer leaf cup having sufficient sensitivity to estimate the high stomatal resistances encountered with pineapple (Aubert, 1971; Neales et al., 1968) was not without its problems. Primary among them was the finding that negative resistances were obtained early in the day when stomata were presumed to be wide open. Minimum positive resistances comparable to those obtained by Aubert (1971) and Bartholomew (1975) were measured after blowing gentle puffs of dry air from a silica gel drying tube on the leaf. It was assumed that sufficient moisture was absorbed by dead trichome cells to give the spuriously low readings obtained without pre-drying the measurement site. Another problem was that the slopes of the calibration curves (Figure 6)

tended to decline (become non-linear) at resistance values in the range of 200 sec cm^{-1}. Because of this fact, leaf resistances in excess of 160 to 170 sec cm^{-1} were assumed to underestimate actual resistances.

Despite the above problems, the instrument used in this study was thought to yield more consistent results at high resistances than other instruments currently available. The relatively high degree of reproducibility of readings at any one time of day obtained with the teflon leaf cup support the assumption that even for values well above 300 sec cm^{-1}, relatively large differences in leaf resistance were real.

The diurnal trends of leaf diffusion resistance of greenhouse-grown plants are shown in Figure 14B and Figure 15B. Corresponding measurements of irradiance and temperature are also shown (Figure 14A and Figure 15A). The general pattern of response of leaf diffusive resistance paralleled that of irradiance and temperature. These results are evidence, not only for the effective suppression of water vapor loss from pineapple during the day, but, because of the reduction in leaf resistance at night, also for the characteristic 'inverted' pattern of stomatal opening observed in many succulent plants, including pineapple. Several workers (Aubert, 1971; Ehrler, 1969; Nishida, 1963; Ting et al., 1967) have shown that the phenomenon of nocturnal stomatal opening is typical of plants having Crassulacean acid metabolism (CAM) characteristics, and correlates with accumulation of organic acids. Pineapple has

FIGURE 14. A. AIR TEMPERATURE AND LIGHT INTENSITY IN THE GREENHOUSE.
B. DIURNAL TRENDS OF LEAF RESISTANCE TO WATER VAPOR TRANSFER IN PINEAPPLE UNDER 5 LEVELS OF STRESS. OBSERVATIONS WERE TAKEN ON FEBRUARY 22-23, 1975. EACH LEAF RESISTANCE VALUE IS A MEAN OF 3 OBSERVATIONS. VERTICAL LINES INDICATE STANDARD DEVIATIONS.

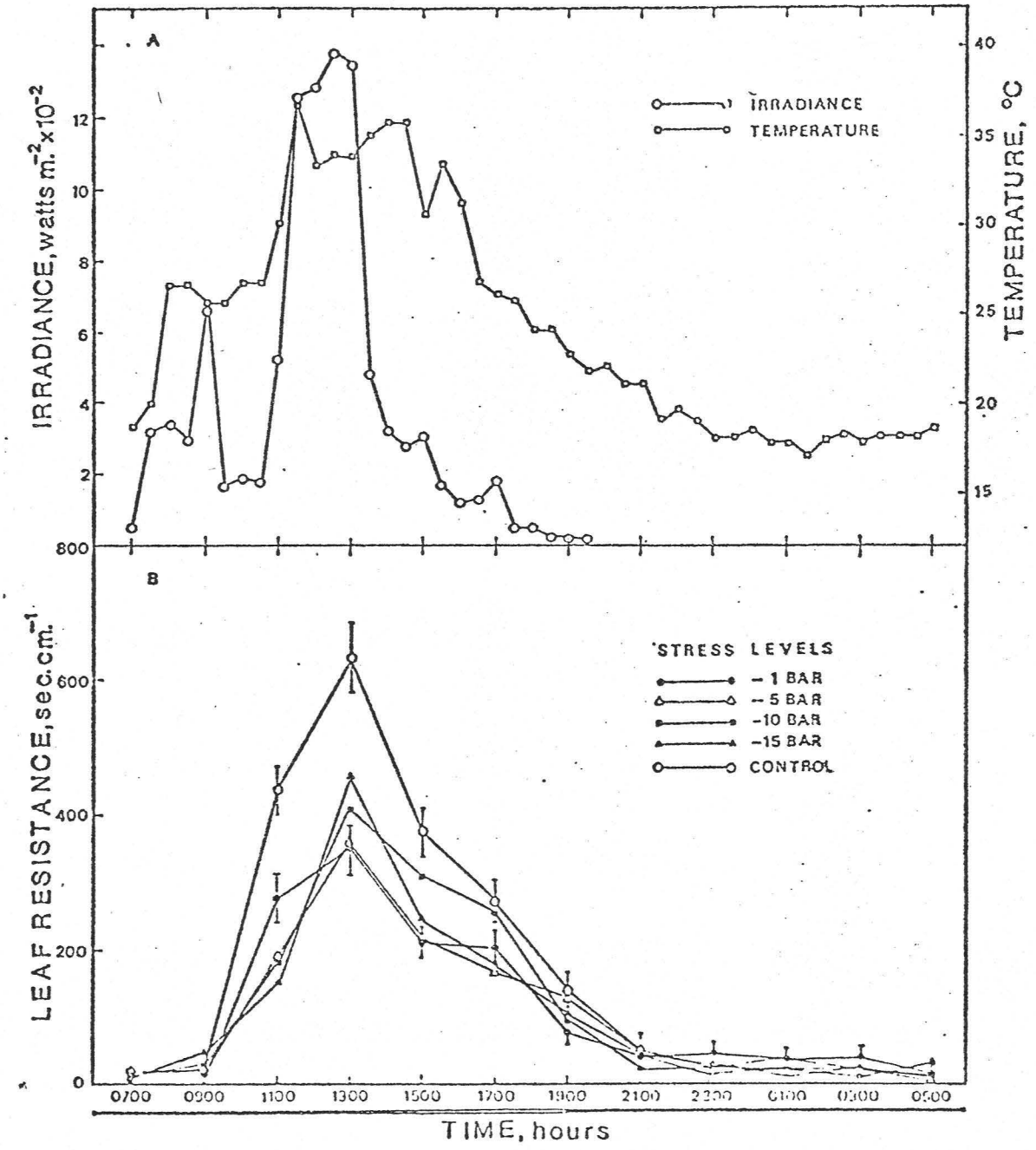
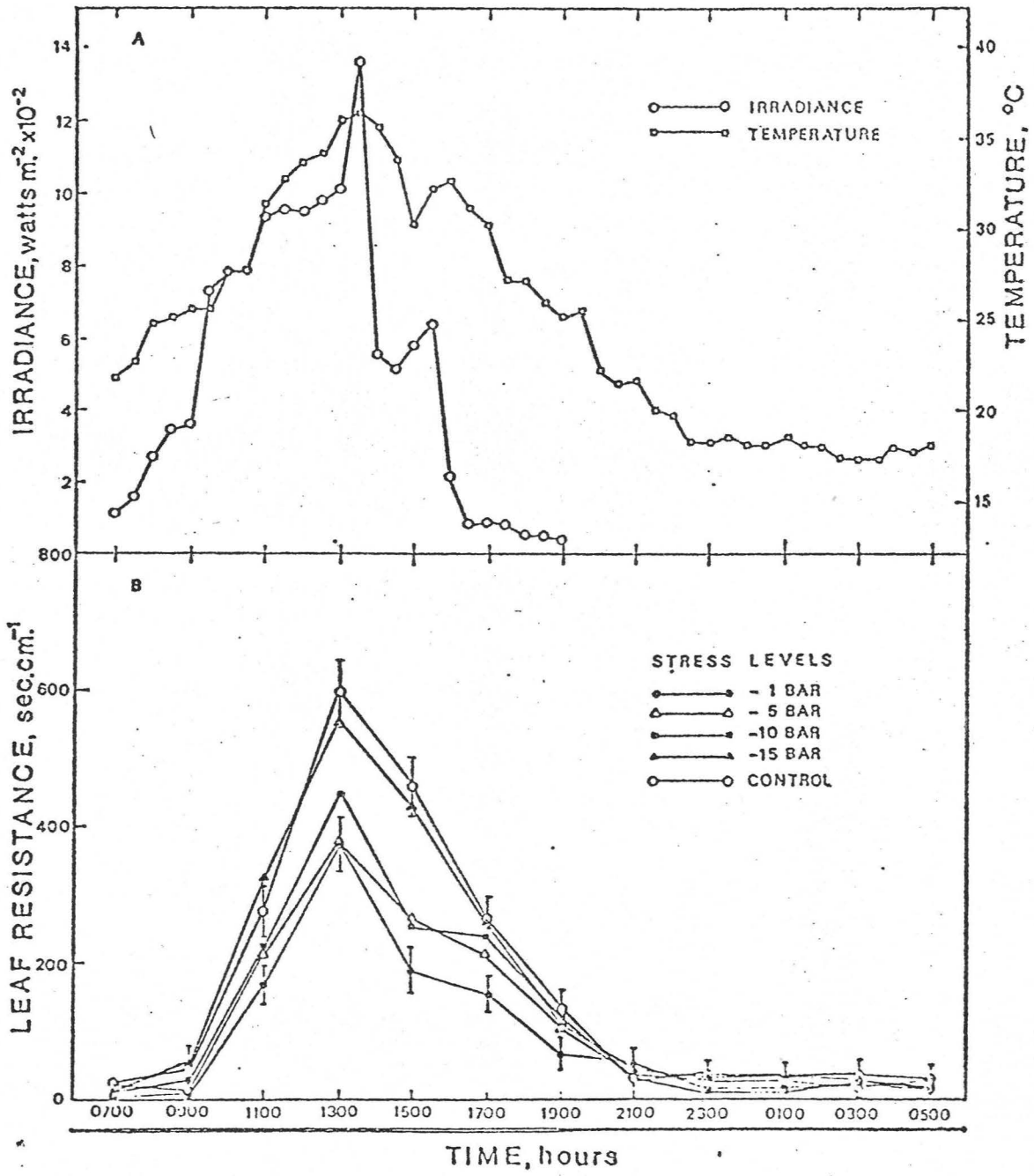

A
IRRADIANCE
TEMPERATURE
IRRADIANCE, watts m⁻² x10⁻²
TEMPERATURE, °C
B
STRESS LEVELS
-1 BAR
-5 BAR
-10 BAR
-15 BAR
CONTROL
LEAF RESISTANCE, sec.cm⁻¹
TIME, hours

FIGURE 15. A. AIR TEMPERATURE AND LIGHT INTENSITY IN THE GREENHOUSE.
B. DIURNAL TRENDS OF LEAF RESISTANCE TO WATER VAPOR TRANSFER IN PINEAPPLE UNDER 5 LEVELS OF STRESS. OBSERVATIONS WERE TAKEN ON APRIL 25-26, 1975. EACH LEAF RESISTANCE VALUE IS A MEAN OF 3 OBSERVATIONS. VERTICAL LINES INDICATE STANDARD DEVIATIONS.


A
IRRADIANCE
TEMPERATURE
IRRADIANCE, watts m^{-2} x10^{-2}
TEMPERATURE, °C
14
12
10
8
6
4
2
800
40
35
30
25
20
15
B
STRESS LEVELS
- 1 BAR
- 5 BAR
-10 BAR
-15 BAR
CONTROL
LEAF RESISTANCE, sec.cm.$^{-1}$
600
400
200
0
0700
0900
1100
1300
1500
1700
1900
2100
2300
0100
0300
0500
TIME, hours

long been known to possess CAM characteristics (Sideris et al., 1948).

Leaf diffusive resistance in all treatments increased sharply from about 0900 hours to 1300 hours and was quite similar to the increase in air temperature (Figure 14). As measurements of leaf resistance were made on a two-hourly basis, it was not known if the values at 1300 hours were the highest attainable. The average maximum and minimum resistances measured on February 22 were 637 and 16 sec cm^{-1} for the unirrigated control plants (Figure 14B). Comparable values for the -1 bar treatment were 351 and 5 sec cm^{-1}. The magnitude of change in measured values of leaf resistance may be influenced by a combination of factors. Bartholomew (1975) indicated that the high leaf resistance values obtained for pineapple were due to high cuticular resistances, few and tight closure of stomata, a long stomatal pore, and the presence of thick mat of trichomes overlying the stomata.

The effects of water stress were evident primarily from the differences in the maximum resistance values reached during the day. The maximum resistances recorded in the -1, -5, -10 and -15 bar treatments on February 22 and 23 were not significantly different although they occurred in order of increasing stress. The mean maximum resistance for the unirrigated control plants was significantly greater than comparable values for the other treatments. Relative water contents for the various treatments, measured on February 25-26 (Figure 12) tended to separate the two

low water (high-stress) treatments better than leaf resistance measurements. Trends in RWC with time of day for the -1, -5 and -10 bar treatments were inconsistent. Climatic data and leaf resistance values obtained on April 25-26 (Figure 15) were similar and both were significantly greater than the other three treatments. As with the February data, the -1, -5 or -10 bar stress did not significantly affect RWC or leaf resistance values. Leaf water potentials measured on April 27 gave the highest level of discrimination between treatments (Figure 11A). Leaf water potentials for the -5, -10, -15 bar stress levels and the unirrigated control were all significantly different from each other.

Leaf resistance values at night were relatively low and overlapped one another. The range of values was from 8 to 49 sec cm^{-1} on February 22, and 7 to 54 sec cm^{-1} on April 25. It is interesting to note that the treatments had no apparent effect on night-time leaf resistances.

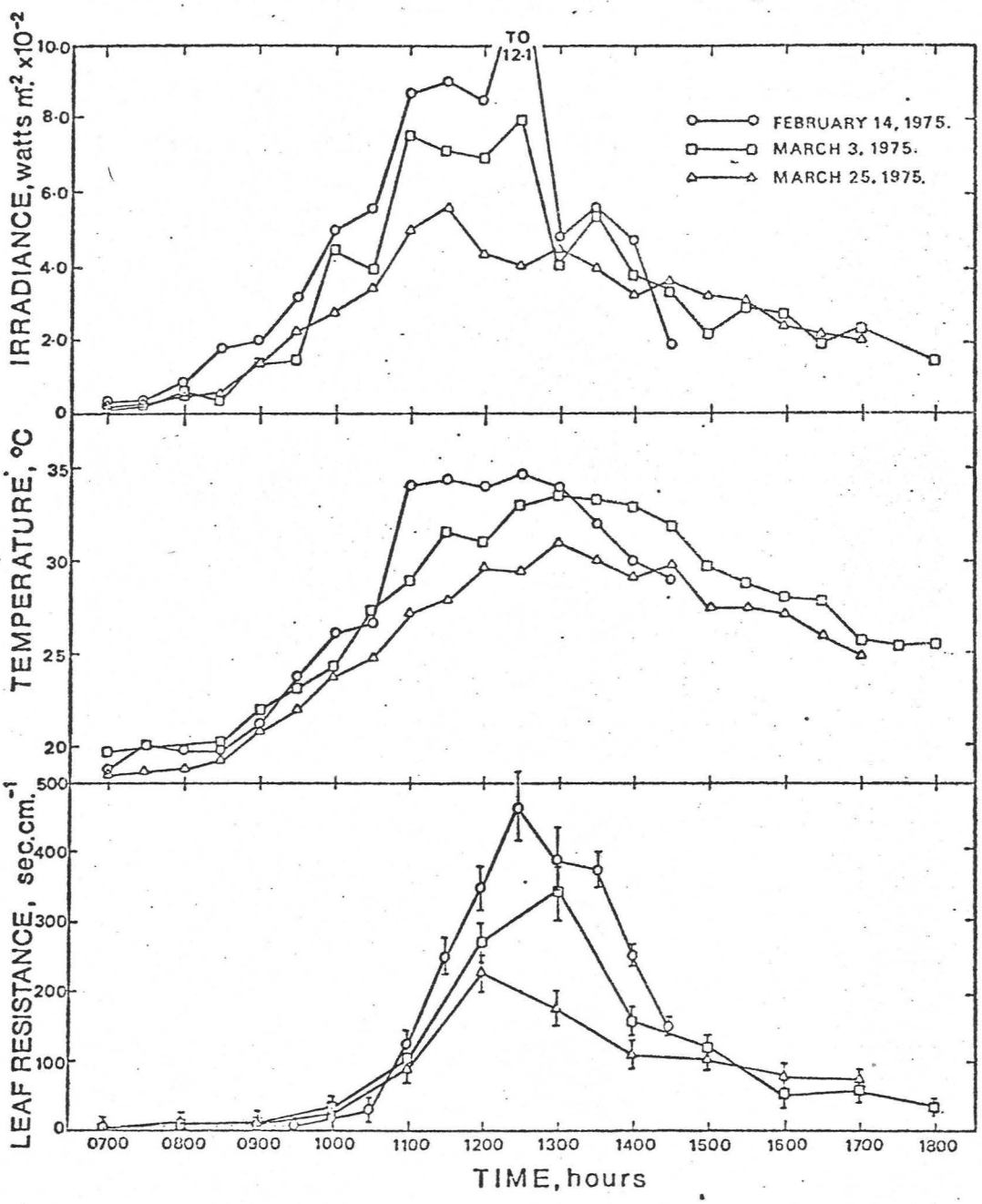
The minimum leaf resistance values recorded in this study were similar to those reported by Aubert (1971) and Bartholomew (1975) but lower than those obtained by Neales et al. (1968). Neales et al. (1968) calculated diffusive resistance by the method of Slatyer and Bierhuizen (1964) and reported minimum values of about 80 sec cm^{-1} in the dark and during the later part of the light period.

There are few data available on the relationship between leaf resistance and net carbon dioxide assimilation for plants having high stomatal resistances. Neales et al. (1968) showed no net uptake of carbon dioxide when leaf resistance for pineapple was near 300 sec cm^{-1}. Some uptake was measured when leaf resistance was nearly 100 sec cm^{-1}. Since carbon dioxide assimilation data were not obtained in this study, the effect of stress on photosynthesis is not ascertainable. If it can be assumed that night opening of stomata was indicative of an actively functioning CAM pathway, then water stress, even to very high levels for prolonged periods, apparently had little or no effect on dark assimilation of carbon dioxide. Increasing dry matter production with decreasing stress (Table IV) could be due to greater carbon assimilation in the light or to a CAM pathway which operated more efficiently.

LEAF DIFFUSION RESISTANCE OF FIELD GROWN PLANTS

Leaf diffusion resistance measurements were made on field grown plants on February 14, March 3 and March 25 (Figure 16). Corresponding irradiance and air temperature (obtained with an exposed mercury thermometer) data are also shown. February 14 was a clear sunny day with maximum irradiance of 1210 w m^{-2}, March 3 was partly cloudy with maximum irradiance of 800 w m^{-2}, and March 25 was heavily overcast with a maximum irradiance of 600 w m^{-2}. Air temperatures correspond well with the measured levels of

FIGURE 16. THE TREND OF LEAF RESISTANCE TO WATER VAPOR TRANSFER IN PINEAPPLE AND OF AIR TEMPERATURE AND LIGHT INTENSITY UNDER FIELD CONDITIONS ON FEBRUARY 14, MARCH 3, AND MARCH 25, 1975. EACH LEAF RESISTANCE VALUE IS A MEAN OF 5 OBSERVATIONS. VERTICAL LINES INDICATE STANDARD DEVIATIONS.


IRRADIANCE, watts m^{-2} x10^{-2}
10·0
8·0
6·0
4·0
2·0
0
TO 12·1
FEBRUARY 14, 1975.
MARCH 3, 1975.
MARCH 25, 1975.
TEMPERATURE, °C
35
30
25
20
LEAF RESISTANCE, sec.cm.$^{-1}$
500
400
300
200
100
0
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800
TIME, hours

irradiance. Dew on the leaves precluded night-time and early morning measurements, while daytime measurements were interrupted occasionally by intermittent showers.

Stomatal resistances of field grown plants showed the characteristic inverted pattern of stomatal opening observed for greenhouse plants (Figure 14 and Figure 15). The maximum and minimum resistance values measured in the field were quite comparable to values for non-stressed greenhouse plants and show that although growth of the plants in the greenhouse was retarded by unknown factors, stomatal responses of the plants were quite normal. Minimum resistances measured at 0700 hours were near 7 sec cm^{-1} and values were similar on all three dates. Changes in leaf resistance with time of day paralleled changes in air temperature, irradiance, and, although it was not measured, presumably relative humidity. The maximum resistance recorded on February 14, a sunny day with high air temperatures, averaged 468 sec cm^{-1}. On March 25, a cloudy day with moderate air temperature, the average maximum resistance reached 228 sec cm^{-1}. Similar data for field grown pineapple have been reported (Aubert, 1971) although the maximum resistances measured in this study were about four times those measured by Aubert (1971). The higher resistances measured in this study could be due to differences in cultivar, environment or instrumentation.

The climatic factor primarily responsible for the marked increase in mid-day resistance values with increasing irradiance

and temperature was not apparent from the results of this study. Aubert (1971) reported that leaf resistances during the early morning were relatively high and those measured at mid-day relatively low on days when irradiance was low and leaf to air temperature gradients were small. Conversely, when irradiance and leaf to air temperature gradients were high, resistance values were low early in the morning and high at mid-day. Aubert (1971) showed that organic acid accumulation and, therefore, presumably net carbon dioxide assimilation, in the dark was greatest under conditions of high irradiance and temperature but he was unable to isolate the factor(s) primarily responsible for the observed variation. Yoder (1969) reported that pineapple transpiration rates during a day when temperatures were 35 C and evaporative demand was high were much lower than transpiration rates during a 25 C day when evaporative demand was lower. The study was conducted under controlled conditions so light was not a variable.

High leaf resistances observed in the experiment on the sunny day and the low transpiration rates observed by Yoder (1969) at 35 C at mid-day would correspond approximately to the period when evaporative demand was greatest. The effects of humidity on stomatal opening have not been adequately investigated on a wide range of species. Hall and Kaufmann (1975) reported that the stomata of sesame responded to humidity at 20 C but not at 34 C. They indicated that at mid-day, when the temperatures were high, the combined effects of large humidity gradients, water stress,

and high temperature might be responsible for the substantial increase in leaf resistance. Increased leaf resistance due to stomatal closure in response to increased humidity gradients was shown to improve water use efficiency (Hall and Kaufmann, 1975). The extent to which humidity gradients influence leaf resistance to water vapor transfer in pineapple cannot be deduced from the data collected in this study. While the factors which affect or control stomatal resistance of pineapple are not so well understood, high leaf resistance values which correspond to large humidity gradients and vice versa would seem to offer significant adaptive advantages to the pineapple plants.

The data in this study show that pineapple has a complex multi-stage mechanism for controlling water loss during the day under conditions where stomatal opening in the dark is relatively unaffected. The primary mechanism of restricting water loss during the day, more or less regardless of prevailing environmental conditions, is the inverted stomatal rhythm. A secondary mechanism appears to be activated by high temperature, low relative humidity, or both, and results in much higher leaf resistance on days when the vapor pressure gradient from leaf to air would be the steepest. The increase in leaf resistance which occurred for greenhouse plants grown at high and low water potentials suggests that still a third mechanism was operating when pineapple plants were subjected to moisture stress. The leaf resistance became so high that there was a likelihood that instrument leakage rather than

cutcular resistance was being measured.

One of the original objectives of the study was to evaluate the relationship between plant water status and stomatal resistance. It was thought that stomatal resistance might prove to be a suitable indicator of plant water status and thus be useful in irrigation scheduling on pineapple plantations where limited water supplies require careful management to assure maximum efficiency. The large variation in stomatal resistance with varying environmental factors superimposed on large diurnal changes would make it very difficult to utilize diffusive resistance as an indicator of plant water status. Preliminary data obtained in two pineapple fields on Maui (Table VII) demonstrates the relative inadequacy of leaf resistance as a means of discriminating between plants having differing leaf water potentials. Soil samples were collected and gravimeteric water contents determined but the key to sample locations was lost so soil water content could not be related to plant water status. The soil in the unirrigated site was, however, much drier to the touch than the site which had been irrigated after planting. These field data support the observation made previously, that plant water potential provided the most sensitive means of discriminating between plants growing in soils having differing water contents.

TABLE VII

LEAF RESISTANCE TO WATER VAPOR TRANSFER (r_1) AND TOTAL LEAF WATER POTENTIAL IN PINEAPPLE UNDER TWO FIELD CONDITIONS ON MAUI ON MAY 15

TIME (HOURS)	IRRIGATED FIELD r_1	S.D.	UNIRRIGATED FIELD r_1	S.D.	OLD FIELD r_1	S.D.
0945	89.9	21.1	...	...	...	...
1030	...	...	207.4	37.6	...	...
1130	...	...	...	...	359.2	77.9
1145	195.4	35.3	...	...	...	...
1350	...	...	215.4	26.2	...	...
1430	243.2	101.5	...	...	...	...
1500	...	...	...	...	107.2	89.0
1520	112.0	52.7	...	...	...	...
1615	56.8	9.5	...	...	...	...
1630	...	...	...	...	73.3	63.0
MEAN LEAF WATER POTENTIAL* (BAR)						
	-9^a		-12^b		-9^a	

* Values followed by a common letter are not significantly different.

S.D. - Standard deviation.

SUMMARY AND CONCLUSION

The pineapple plant has an interesting combination of traits that are characteristic of xerophytic plants. It is one of the most important crop plants, among very few others, to survive long periods of water stress.

The present study was designed to examine the response pattern shown by pineapple to conditions of increasing soil moisture stress. The magnitude of three of the indicators commonly used to indicate plant water status, namely, leaf water potential and its components, relative water content, and leaf diffusion resistance were measured on plants grown at 5 levels of stress.

Water stress has a marked effect on all plant processes. It has also been expected that water stress effects would be more pronounced on active processes which have their expression in elongation or vegetative growth. The pineapple is no exception. Plant growth was affected signficantly by water supply. Dry matter production increased with decreasing stress.

As soil moisture stress increased, total leaf water potential, estimated by a dye technique, decreased curvilinearly. The maximum value reached in the -1 bar treatment was -6 bars, while the minimum in the unirrigated control was -22 bars. The dye technique, through somewhat limited in accuracy, proved adequate for the measurement of relative values and changes

in plant water potential of pineapple. Osmotic potential was measured with a Wescor psychrometer using extracted leaf sap. Osmotic potential values did not differ significantly between treatments and were on the order of -13 to -15 bars. The corresponding turgor potential values ranged from +7 bars to -9 bars. The values were in agreement with data presented by other workers.

Decreased plant turgor which accompanied increases in soil moisture stress caused decreases in RWC. The diurnal trend of RWC within treatments was not different. Maximum values reached in the unirrigated control ranged from 69 to 78 percent, and maximum values for the well-watered treatment were as high as 96 percent. Relative water content was a rather insensitive indicator of water stress in pineapple, particularly when water deficits were not extremely severe.

The estimation of leaf resistance to water vapor transfer was made possible with the development of a porometer leaf cup. The design and calibration of the porometer are described. The diurnal trend in leaf diffusion resistance measured with the prormeter was high in the light and low in the dark. The observed inverted pattern was typical of those described for plants having Crassulacean acid metabolisn (CAM).

Under greenhouse conditions, daytime leaf resistance values between the well-watered and the unirrigated control were significantly different. The maximum average value reached during the day was about 360 sec cm^{-1} for the -1 bar treatment. The

unirrigated control had maximum values over 600 sec cm^{-1}. Treatment effects on minimum values attained during the night and early morning hours were not apparent. Leaf diffusion resistances of plants in the field observed during the daylight hours were dependent on meteorological conditions. Maximum values reached were over 400 sec cm^{-1}, while the minimum values were about 7 sec cm^{-1}. These values were quite similar to those measured on low-stress plants grown in the greenhouse.

Pineapple has been grown in areas where the potential evaporative demand is greater than the annual rainfall. Successful culture of this crop plant is attributed to its physiological modifications which enable the plant to survive periods of severe water stress. Pineapple uses only one-tenth as much water per unit of dry matter produced as most other crop plants (Ekern, 1965). This efficient use of water is of particular importance where water supplies can limit maximum production. The low water-use rate of pineapple is related to the inverted pattern of stomatal resistance and physiological mechanisms which couple leaf resistance more or less directly to daytime leaf temperatures and evaporative demand.

In evaluating the water status of the plant to predict the influence of environmental factors upon plant growth when water is limiting, measurements of the plant-soil-atmosphere components are necessary. Quantitative relationships between leaf water potential (and its components), relative water content, and leaf diffusion resistance to water vapor transfer, and other parameters

indicating the effects of water stress not observed in this study would be a subject of great interest for future research with pineapple. Such relationships would allow the prediction of growth and yield reduction in crops of this nature as a result of water stress.

APPENDIX

TABLE VIII

EFFECTS OF EQUILIBRATION TIME ON TOTAL LEAF WATER POTENTIAL OF PINEAPPLE LEAF TISSUE FROM THE UNIRRIGATED CONTROL AND THE -1 BAR TREATMENTS

EQUILIBRATION TIME (HOURS)	UNIRRIGATED CONTROL MEAN(BARS)	S.D.	-1 BAR MEAN(BARS)	S.D.
1	24	2.1	9	1.9
2	24	2.1	7	1.9
3	23	1.4	8	1.0
4	22	1.4	8	1.0
5	22	1.2	7	1.7
6	21	1.4	8	1.3
7	22	1.2	8	1.2
8	22	1.3	6	1.5

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	Mean Squares	
Unirrigated Control			
Between Equilibration Time	7	5.40	n.s.
Within Equilibration Time	32	9.33	
-1 Bar Treatment			
Between Equilibration Time	7	4.69	n.s.
Within Equilibration Time	32	3.51	

S.D. - Standard Deviation.

n.s. - Not significant.

TABLE IX

EFFECTS OF EQUILIBRATION TIME ON RELATIVE WATER CONTENT OF PINEAPPLE LEAF TISSUE FROM THE UNIRRIGATED CONTROL AND THE -1 BAR TREATMENTS

EQUILIBRATION TIME (HOURS)	UNIRRIGATED CONTROL MEAN (BARS)	S.D.	-1 BAR MEAN (BARS)	S.D.
1	80.8	3.6	96.0	3.2
2	75.4	3.2	93.2	3.2
3	71.4	3.2	94.0	2.4
4	69.2	2.8	92.0	3.3
5	68.6	2.0	91.4	2.0
6	67.6	2.8	92.0	2.2
7	68.8	2.2	92.8	2.8
8	69.0	2.7	93.2	2.0

ANALYSIS OF VARIANCE

Source of Variation	Degrees of Freedom	Mean Square
Unirrigated Control		
Between Equilibration Time	7	6.27 n.s.
Within Equilibration Time	32	3.56
-1 Bar Treatment		
Between Equilibration Time	7	19.82*
Within Equilibration Time	32	8.09

S.D. - Standard Deviation

n.s. - Not significant

* - Significant at P = 0.05

TABLE X

EFFECTS OF SOIL WATER POTENTIAL ON TOTAL LEAF WATER POTENTIAL IN PINEAPPLE ON APRIL 12, APRIL 16 AND APRIL 27, 1975

SOIL WATER POTENTIAL (BARS)	MEAN TOTAL WATER POTENTIAL (BARS) APRIL 12	APRIL 16	APRIL 27
- 1	- 6	- 7	- 7
- 5	- 6	- 9	- 8
-10	- 9	-10	-11
-15	-14	-15	-15
-18[c]	-23	...	...
-19[c]	...	-21	...
-21[c]	.-.	...	-22

ANALYSIS OF VARIANCE

Source of Variation	Degree of Freedom	Mean Squares
Between Replicates (dates)	2	1.4
-1 vs -5 bar treatment	1	1.5 n.s.
-5 vs -10 bar treatment	1	8.2**
-10 vs -15 bar treatment	1	32.7**
-15 vs control treatment	1	80.7**
Residual	8	0.9

c - Unirrigated control

** - Significant at P = 0.01

n.s. - Not significant

TABLE XI

EFFECTS OF SOIL WATER POTENTIAL ON OSMOTIC POTENTIAL IN PINEAPPLE ON APRIL 12, APRIL 16 AND APRIL 27, 1975

SOIL WATER POTENTIAL (BARS)	MEAN OSMOTIC POTENTIAL (BARS) APRIL 12	APRIL 16	APRIL 27
-1	-13.0	-14.2	-14.83
-5	-13.4	-13.2	-14.16
-10	-14.65	-14.27	-13.53
-15	-14.73	-13.07	-13.83
-18[c]	-13.8	...	...
-19[c]	...	-13.87	...
-21[c]	...	...	-14.6

ANALYSIS OF VARIANCE

Source of Variation	Degree of Freedom	Mean Squares
Between Replicates (dates)	2	0.28 n.s.
Treatment	4	0.16 n.s.
Residual	8	0.5025

c - Unirrigated control
n.s. - Not significant

TABLE XII

EFFECTS OF SOIL WATER POTENTIAL ON TURGOR POTENTIAL IN PINEAPPLE ON APRIL 12, APRIL 16 AND APRIL 27, 1975

SOIL WATER POTENTIAL (BARS)	TURGOR POTENTIAL (BARS) APRIL 12	APRIL 16	APRIL 27
-1	+7.0	+7.2	+7.83
-5	+7.4	+4.2	+6.16
-10	+5.65	+4.27	+2.53
-15	+0.73	-1.93	-1.17
-18[c]	-9.2	...	...
-19[c]	...	-7.13	...
-21[c]	...	...	-7.4

ANALYSIS OF VARIANCE

Source of variation	Degrees of Freedom	Mean Squares
Between Replicates (dates)	2	1.33 n.s.
Treatments		
-1 vs -5 bar	1	3.03 n.s.
-5 vs -10 bar	1	4.70 n.s.
-10 vs -15 bar	1	16.90 *
-15 vs control	1	113.50 **
Residual	8	1.76

c - Unirrigated control.
n.s. - Not significant.
* - Significant at P = 0.05
** - Significant at P = 0.01

TABLE XIII

RELATIVE WATER CONTENT (PERCENT) IN PINEAPPLE AT 5 LEVELS OF STRESS MEASURED ON FEBRUARY 25 AND 26 EACH VALUE IS A MEAN OF 5 OBSERVATIONS

TREATMENT (BAR)	TIME (HOURS) 0700	1100	1500	1900	2300	0300
-1	95.2	95.1	94.6	93.8	94.1	96.4
-5	95.5	92.4	93.4	94.3	91.8	94.8
-10	92.2	91.3	91.8	89.0	93.5	90.1
-15	91.4	88.5	88.1	86.0	86.9	87.3
CONTROL	84.6	81.1	82.3	79.4	77.2	78.4

ANALYSIS OF VARIANCE

Source of Variation	Degree of Freedom	Mean Squares
Time of day	5	6.97 n.s.
Treatment		
- 1 vs - 5 bar	1	4.69 n.s.
- 5 vs -10 bar	1	20.45 n.s.
-10 vs -15 bar	1	38.8 *
-15 vs control	1	204.3 **
Residual	20	7.95

n.s. - Not significant
* - Significant at P = 0.05
** - Significant at P = 0.01

TABLE XIV

RELATIVE WATER CONTENT (PERCENT) IN PINEAPPLE AT 5 LEVELS OF STRESS MEASURED ON APRIL 28 AND 29 EACH VALUE IS A MEAN OF 5 OBSERVATIONS

TREATMENT (BAR)	TIME (HOURS) 0700	1100	1500	1900	2300	0300
-1	95.0	94.1	91.4	89.4	93.2	96.1
-5	93.2	91.2	88.8	90.3	92.0	91.1
-10	92.1	92.2	86.1	87.5	90.4	90.3
-15	86.4	84.7	76.5	78.0	82.5	84.4
CONTROL	76.0	72.2	69.1	71.1	70.4	73.4

ANALYSIS OF VARIANCE

Source of Variation	Degree of Freedom	Mean Squares
Time of day	5	28.26 **
Treatments		
-1 vs -5 bar	1	15.88 *
-5 vs -10 bar	1	6.4 n.s.
-10 vs -15 bar	1	212.5 **
-15 vs control	1	363.61 **
Residual	20	1.97

n.s. - Not significant
* - Significant at P = 0.05
** - Significant at P = 0.01

TABLE XV

LEAF RESISTANCE TO WATER VAPOR TRANSFER (r_1) IN PINEAPPLE UNDER 5 LEVELS OF STRESS ON FEBRUARY 22 AND 23, 1975

TIME (HOURS)	-1 BAR		-5 BARS		-10 BARS		-15 BARS		CONTROL	
	r_1	S.D.	r_1	S.D.	r_1	S.D.	r_1	S.D.	r_1	S.D.
0700	5.4	3.6	8.3	4.6	13.8	3.2	6.1	3.2	16.2	7.3
0900	13.3	10.8	22.9	11.9	27.1	9.1	44.0	12.9	17.6	6.2
1100	277.3	69.3	191.9	32.4	117.5	35.8	150.4	25.6	437.8	74.3
1300	351.0	75.1	357.1	52.6	407.7	54.3	554.6	68.3	637.2	106.2
1500	210.7	47.3	218.5	67.2	306.5	72.4	245.2	51.1	375.6	74.7
1700	202.7	53.3	165.3	39.4	253.2	61.8	176.0	23.7	268.0	64.0
1900	74.6	36.9	125.5	30.1	90.6	32.6	102.5	19.2	138.7	58.7
2100	37.3	25.6	43.7	24.8	20.9	11.3	40.2	18.9	48.6	42.7
2300	42.8	32.1	16.2	15.7	27.1	11.4	29.3	8.4	23.0	18.4
0100	32.0	37.6	23.2	18.6	17.8	6.7	10.4	6.5	37.3	27.1
0300	38.9	31.8	23.8	19.3	10.9	7.3	22.1	11.0	20.9	16.8
0500	12.8	4.3	11.3	6.7	32.5	12.4	8.1	3.9	6.2	4.4

S.D. - Standard deviation.

TABLE XVI

LEAF RESISTANCE TO WATER VAPOR TRANSFER (r_1) IN PINEAPPLE UNDER 5 LEVELS OF STRESS ON APRIL 25 AND 26, 1975

TIME (HOURS)	-1 BAR		-5 BARS		-10 BARS		-15 BARS		CONTROL	
	r_1	S.D.	r_1	S.D.	r_1	S.D.	r_1	S.D.	r_1	S.D.
0700	2.7	1.4	14.2	3.6	10.2	3.1	13.3	2.5	21.6	11.9
0900	8.0	2.3	10.7	2.9	29.4	10.6	50.9	26.7	45.3	42.6
1100	168.0	58.6	213.6	61.4	224.0	53.4	325.3	68.4	273.7	72.0
1300	378.0	77.3	379.6	72.8	445.3	70.9	551.9	75.1	604.8	98.7
1500	184.1	69.2	266.1	59.3	250.7	63.3	426.7	61.8	458.9	85.3
1700	154.9	52.9	213.3	58.7	234.7	60.8	256.0	58.4	259.4	61.3
1900	119.2	38.1	102.4	42.2	120.6	37.8	112.0	22.9	129.2	63.9
2100	54.3	42.7	31.9	15.6	36.8	11.2	40.2	20.7	26.7	21.3
2300	16.2	11.3	13.8	4.9	6.4	1.8	29.1	6.8	32.4	18.7
0100	13.3	7.8	21.6	4.7	9.7	6.9	31.2	12.4	32.8	30.8
0300	20.9	3.5	11.9	5.4	5.4	9.2	29.7	11.8	33.1	18.7
0500	7.2	4.1	20.8	12.8	11.5	4.3	20.0	10.3	25.6	31.8

S.D. - Standard deviation.

TABLE XVII

LEAF RESISTANCE TO WATER VAPOR TRANSFER (r_l) IN PINEAPPLE UNDER FIELD CONDITIONS ON FEBRUARY 14, MARCH 3, AND MARCH 25, 1975

TIME (HOURS)	FEBRUARY 14		MARCH 3		MARCH 25	
	r_l	S.D.	r_l	S.D.	r_l	S.D.
0700	7.46	2.3	6.9	4.6	6.7	4.4
0800	8.1	4.0	9.7	5.3	11.7	9.1
0900	9.3	6.7	13.4	4.2	10.6	5.3
0930	7.7	6.3	...	...	...	...
1000	16.0	10.9	34.6	31.9	26.7	13.3
1030	27.8	37.3	...	...	...	...
1100	121.9	42.6	103.9	38.7	87.6	37.3
1130	251.2	53.3	...	...	...	...
1200	351.1	64.0	271.8	47.9	227.9	58.6
1230	468.4	101.3	...	...	...	...
1300	389.6	90.6	341.1	79.9	175.4	49.7
1330	378.0	50.6	...	...	...	...
1400	252.3	32.0	154.6	42.8	110.6	41.9
1430	151.1	29.3	...	...	...	...
1500	...	...	118.6	18.7	102.1	27.6
1600	...	...	50.6	16.0	77.8	36.8
1700	...	...	56.0	31.9	74.2	32.2
1800	...	...	31.9	25.8	...	...

S.D. - Standard deviation.

TABLE XVIII

TOTAL LEAF WATER POTENTIAL (BARS) IS PINEAPPLE UNDER FIELD CONDITIONS ON MAUI ON MAY 15

	IRRIGATED	UNIRRIGATED	OLD FIELD
	9	11	9
	8	13	9
	8	10	8
	9	13	9
	9	...	...
MEAN	8.6	11.75	8.75

ANALYSIS OF VARIANCE

Source of Variation	Degree of Freedom	Mean Squares
Between Treatments	2	13.19*
Within Treatment	10	0.87

Comparisons

Irrigated vs Old Field : t = 0.24 n.s.
Irrigated plus Old Field vs Unirrigated : t = 5.04*

* - Significant at P = 0.05.

n.s. - Not significant.

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